Modeling the Effects of Roadside and Meadow Foliage Management on the Dynamics of *Bombus impatiens* Populations

A Thesis
by
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Abstract

Populations of pollinators, including the common ground bumble bee *Bombus impatiens*, can be inhibited or suffer declines due to a lack of readily available flower resources. Flower resources can be influenced by a variety of natural and anthropogenic factors. There is evidence to suggest that regimented foliage management significantly alters the availability of pollinator-relevant flowers. Here I report on field studies testing the effects of foliage management (mowing) on the abundance of five bumble bee-relevant flowering plant species with diverse life histories. I then outline a mathematical model I developed based on *B. impatiens* life history to predict the impacts of mowing regimes on the bees' population dynamics.

I used flower phenology surveys to determine the inflorescence density of each of my five target flower species within two ecologically different habitat types under different foliage management regimes. These surveys indicated that intentionally cutting back foliage (i.e. mowing roadside grasslands and meadows) significantly reduced the overall number of inflorescences when all target flowers were considered as one group. When considered individually, only the flower species *Solidago rugosa* showed significant reduction due to mowing treatment. This observation suggests that foliage management has a negative effect on the density of flowering plants when implemented in this way. In many cases the degree of foliage management was so severe that no flowers ever came into bloom within the study sites.

I then incorporated inflorescence density data into mathematical projections of the total nectar produced within an explicit landscape under different hypothetical foliage management

regimes. The outcomes of this model suggest that implementing mowing practices influence the ability of *Bombus impatiens* to produce new queens and thus to their ability to persist in relatively higher abundance.

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CHAPTER I

GENERAL INTRODUCTION

Insects are the most diverse taxa of terrestrial animals and are found in virtually every environment around the globe. There are more than one million described species of insects, and an estimated four million undescribed (Gill et al. 2016). Insect pollinators are one of the most beneficial taxa to humanity, where pollination services that wild and managed pollinators provide an estimated worth of more than 200 million dollars annually (Blaauw & Isaacs 2014). It is estimated that total global crop yields could decline anywhere from 3-8% in the total absence of animal-mediated pollination (Bretagnolle & Gaba 2015). The prevalence of pollination-dependent crop farming is expected to increase in upcoming years, due to an increased demand for food by a growing human population (Garibaldi et al. 2016). Despite their demonstrated importance, pollinators are experiencing declines worldwide, largely due to anthropogenically driven factors (Carvell 2002, Gill et al. 2016, Goulson, Lye & Darvill 2008, Goulson, Nicholls, Botias & Rotheray 2015, Potts et al. 2010, Potts et al. 2016, Vanbergen & Insect Pollinators Initiative 2013, Williams & Osbourne 2009). The specific mechanism is likely a combination of multiple stressors happening concurrently (Gill et al. 2016), including climate change (Hegland, Nielsen, Lazaro, Bjerknes & Totland 2009), habitat fragmentation (Hadley &

Betts 2012), land-use change (Kremen, Williams & Thorp 2002), use of agrochemicals (Hladik, Vandever & Smalling 2016), the presence of invasive species (Goulson 2003b), and a lack of appropriate floral resources (Bretagnolle & Gaba 2015).

Bumble bees, *Bombus spp.*, are particularly important pollinators for agriculture due to their high rates of pollination efficiency relative to other visitors for many crops (Artz & Nault 2011). Though complete data is lacking in North America, the largest study to date of eight species showed that half had experienced significant range constrictions, occupying 23-87% less area than in historical records. This range restriction has occurred simultaneously with a 96% reduction in abundance for these four species (Cameron et al. 2011). Declines of bumble bees in Europe and North America have been largely attributable to the intensification of agricultural practices that prioritize mass production of monocultures. These practices decrease the diversity and abundance of floral resources relevant to bumble bee species (Goulson et al. 2008). Specifically, the conversion of unimproved grasslands, which provide suitable habitat for bumble bees, to monoculture grass plots for use as grazing material or hay production has resulted in a considerable loss of resources for these pollinators (Goulson et al. 2008). There is evidence that suggests that forage plants for bumble bees have experienced declines that are disproportionate to the declines of plants not used by bumble bees (Goulson et al. 2008). Other changes in agricultural practices also provide evidence about the causes for the decline of bumble bees. For instance, the use of legumes, specifically clover species which are highly valued as forage resources for bumble bees, as a rotation crop has been largely abandoned since the use of nitrogenous fertilizers has become more relied upon by modern agricultural practices (Goulson et al. 2008).

The incentive for pollinators visiting flowers to facilitate pollen transfer originates from the nutritional rewards the plants produce; nectar provides a source of carbohydrates and pollen provides protein. Bumble bees and other pollinators rely on floral resources for all of their nutrient input. In native habitats with diverse floral resources, individual bumble bee foragers "major and minor" in collecting resources from one or a few species, but the colony as a whole generalizes on a broader range of the floral community (Heinrich 1975), thus diversifying the nutritional makeup of their diets. The nectar and pollen that an individual plant produces varies greatly. Factors that can affect nectar and pollen production include plant species life history (Heil 2011; Jakobsen & Kristjansson 1994), individual plant phenotype (Jakobsen & Kristjansson 1994; Boose 1997), air temperature (Heil 2011; Jakobsen & Kristjansson 1994), humidity (Heil 2011), other environmental conditions (Boose 1997), consumption rates by nectarivores (Heil 2011), and floret age (Jakobsen & Kristjansson 1994).

When considering the patch level ability of plants to provide rewards for bumble bees, there are several key components, some of which are: floral density, floral composition, the spatial arrangement of flowers relative to bee colonies, and individual flower resource production rates (Haussler, Sahlin, Baey, Smith & Clough 2016). Overall, areas that have lower numbers of flowers have lower numbers of bumble bees due to resource deficiencies (Carvell 2002; Haussler et al. 2016). Floral composition can be vitally important to many pollinator species, and not every pollinator will benefit from the same composition. For example, a subset of floral species receive enhanced pollination from bumble bees (Javorek, Mackenzie & Kloet 2002); these plants sometimes invest in providing particularly attractive rewards, such as nectar

with a high sugar content (Heil 2011). Flowers that produce higher quality nectar tend to be visited more often, though resource production (Fowler, Rotheray & Goulson 2016). The presence of mass-flowering crops decreases the abundance of bumblebees, despite positive effects on honey bee populations (Holzchuh et al. 2016). Patches of flowers that are equal in nectar production will be visited more frequently if they are located closer to bee colonies, likely due to the energetic savings for foragers; bee colonies are able to more efficiently gather resources when patches are closer to the colonies (Haussler et al. 2016; Osborne et al. 2008; Williams & Osborne 2009).

My study investigates the effects of land use practices on pollinators (bumble bees) through: (1) empirically testing different foliage management regimes on floral resources important to a common native species, *Bombus impatiens*, and (2) through mathematically modeling how such effects at a landscape scale cascade to impact *B. impatiens* populations. The study was set in Watauga County, NC within Julian Price Memorial Park on land previously used as an agricultural lease and managed by The Blue Ridge Parkway.

The bumble bee *Bombus impatiens* is native to the eastern portions of North America, but due to its usefulness as an agricultural pollinator, and the relative ease of rearing commercial colonies, it has been introduced to other areas (Looney, Strange, Freeman & Jennings 2019). The range in which wild *B. impatiens* are found have been expanding in the Pacific Northwest since their incidental release from greenhouses and field pollination projects (Looney et al. 2019). Yet, within the native range of *B. impatiens* there is competition for resources with other native and invasive pollinators (Graham, Eaton, O'brien & Starks 2019). I selected *B. impatiens* as a focus due to its commonality and because its associations with floral species are well-documented.

Chapter 2 of this study, The Effects of Foliage Management on Floral Abundance, empirically examines the effects of foliage management regimes on floral resources important to *B. impatiens,* by documenting the phenology of *Solidago rugosa*, *Asclepias syriaca*, *Monarda clinopodia*, *Prunella vulgaris*, and *Trifolium pratense* under different mowing treatments.

Bombus impatiens, and other bumble bees, are social insects. Their life cycle is complex and involves a variety of castes within each colony. The queen is the foundation of any *Bombus spp.* nest, as she is the sole reproductive female that is responsible for building and maintaining a colony during flower season (Goulson et al. 2008). At the beginning of spring, bumble bee queens emerge from their winter diapause and begin collecting resources and searching for suitable nest sites. Nest site requirements and preferences differ among bumble bee species. For example, *Bombus pascuorum* tend to nest in grass tufts while *Bombus terrestris* typically nest in underground cavities (Goulson et al. 2008). Some queens will find suitable nests, others will not; nest sites can limit population size for some species (Byron 1980). Once a queen has a nest she begins the arduous process of assimilating resources and laying brood cells to produce workers (Schmid-Hempel & Schmid-Hempel 1998). Once the first batch of workers has been produced, in most temperate species the queen stops foraging, which is now the workers' job, and specializes in producing brood (Goulson 2003a). The workers will collect resources throughout the flowering season and the degree of success for the colony depends on their number and how effective they are at collecting nectar and pollen. The resources that the workers assimilate towards the end of the flowering season are allocated to the production of reproductives by the colony's queen (Goulson 2003a). The number of new queens that each colony produces is reliant on how many resources it was able to assimilate during a critical time of the flowering season

(Goulson et al. 2008). These new queens that are produced mate, disperse, and overwinter to begin the cycle again next year. The old queens die with the workers and drones from their colonies (Goulson et al. 2008). The consequence of this life cycle means that populations of bumble bees, including *B. impatiens*, must be re-establish each year.

Chapter 3, Modeling the Effects of Foliage Management on *Bombus impatiens*, explores through simulation how the dynamics of *B. impatiens* populations might be impacted by foliage management regimes. The complex life cycle of the bumble bee as well as experimental effects of mowing on floral abundance are incorporated into the simulations.

The objectives of this study were to determine whether implementing consistent mowing treatments significantly changed the abundance of target flower species that are known associates with *B. impatiens* and to estimate potential changes in the population of *B. impatiens* due to implementing mowing treatments. This study should be of significant importance to agencies such as the National Park Service, which spend a large portion of their budgets on land management yet also have a vested interest in understanding how management regimes affect wildlife. Here I provide evidence about the ideal way to manage roadside and meadow habitat to support populations of *B. impatiens,* which could be used to optimize mowing strategies and schedules along The Blue Ridge Parkway or beyond. Chapter 3 additionally provides a method for determining the ideal location within a landscape for central place foragers, which could potentially lead to strategies for locating wild colonies of *B. impatiens* or supporting the growth of central place forager colonies.

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CHAPTER II

The Effects of Foliage Management on Floral Abundance

ABSTRACT

The purpose of this experiment was to determine if vegetation management regimes (mowing) would impact inflorescence density of bumble bee food resources in roadside and old field meadow habitat of the Southern Appalachians. I documented the abundance and floral phenology of five plant species: *Solidago rugosa, Asclepias syriaca, Trifolium pratense, Monarda clinopodia,* and *Prunella vulgaris*. I found that there was a significant decline in the total inflorescence density for all flowers as a pooled population when mowing treatments were implemented. When considered as separate populations, the only species that showed a significant decline through time due to mowing was *S. rugosa*. I also found for *S. rugosa* that landscape cover type, mowing treatment, and the interaction between those terms significantly contributed to its abundance through time. All flower species were found in significant abundance during peak flowering week for that plant. All flower species showed a decline in abundance during the week they were most abundant when mowing treatments were implemented. Results from this study should inform how we can best manage habitat to support pollinators. Intense foliage management in the long term could prove detrimental to flower diversity, density and abundance.

INTRODUCTION

Anthropogenic land use is a global phenomena and has been for millennia. Areas across the globe have been altered, landscaped, and selectively destroyed in order to achieve more ideal conditions for human settlement (Ellis 2015). As populations of humans are projected to increase in the near future, land use is projected to increase substantially along side it (Winfree, Bartomeus & Cariveau 2011). Substantial habitat alteration poses a threat to populations of native species that occupied the areas prior to development.

Pollinators, like other native wildlife, require significant area of contiguous habitat that provides substantial food and nesting resources to sustain populations (Bender, Contreras & Fahrig 1998). However, there is mounting evidence that increased land use on a large scale poses a threat to pollinator biodiversity and the ecosystem services these species provide (Cole, Brocklehurst, Robertson, Harrison & McCracken 2015; Mallinger, Gibbs & Gratton 2016). Land use effects on pollinators may be mediated via depletion of floral abundance (Winfree et al. 2011); pollinator population size has been shown to associate more consistently to floral resource availability than to land use alone (Winfree et al. 2011). Anthropogenic land use may alter the abundance of particular flowering plants through a variety of mechanisms including alterations to soil microbe composition (Panke-Buisse, Poole, Goodrich, Ley & Kao-Kniffin 2015), connectedness of appropriate habitat patches (Damschen, Haddad, Orreck, Tewksbury & Levey 2017), use of nitrogenous agrochemicals (Suding et al. 2005), and varying light availability (Kilkenny & Galloway 2008).

A substantial component of land use is groundcover management, usually through mowing. Mowing practices indiscriminately cut plants and can be comparable to intense grazing. Intensely managed grassland fields provide poor resource availability for pollinators (Cole et al. 2015). Frequently mowing grassy habitat within urban areas is also known to negatively impact the abundance and diversity of flower assemblages found therein (Bertoncini, Machon, Pavoine & Muratet 2012). The ideal frequency to mow grassland areas to support floral diversity and abundance, and support pollinators, varies for different habitats. One study found that when managing roadside grassy areas, mowing more frequently (twice per year) is more beneficial than mowing less frequently (once per year) and that clearing the dried plant material from mowed areas is beneficial to flower visiting insects (Noordijk, Delille, Schaffer & Sykora 2009). Alternatively, when managing grassy lawns in suburban environments one study found that mowing at a moderate frequency (every two weeks) was more beneficial for pollinator abundance than mowing at a low frequency (every three weeks) or a high frequency (every one week), despite the increased abundance of flowers in the low frequency treatment (Lerman, Contosta, Milam & Bang 2018). The proposed mechanism for this result is that increased grass biomass and height makes it more difficult for pollinators to locate and manipulate flowers.

This study takes an anthropogenic land use perspective on the preservation of resources for a common native bumble bee pollinator in the Southern Appalachians, *Bombus impatiens*. I asked how intentional management of grassy areas via mowing can change the abundance of flowers relevant to these pollinators. I focused on management of vegetation in two habitats, roadside and old fields, in swaths of land that were formerly under use for agricultural purposes. Mowing grassy areas along roadsides and old fields has the potential to impact pollinator

populations by altering flower resources, but different management regimes might prove more or less detrimental to the floral resources needed to support *B. impatiens*. I expected to find that low growing flowers, such as *Prunella vulgaris*, would suffer less than taller species, such as *Asclepias syriaca*, since the shorter plants might produce flowers low enough to be avoided by mowing or might produce blooms quickly enough to reproduce between mowings. I predicted that implementing mowing treatments would be detrimental overall to the abundance of flowers that produce resources relevant to *B. impatiens*.

MATERIALS AND METHODS

Study Location

This study was conducted on land managed by The Blue Ridge Parkway in Watauga County, North Carolina, from May to October 2018. The study sites were located within Julian Price Park along Old Johns River Road (coordinates: 36°08’18”N, 81°43’21”W). Areas near the access road that were not separated from the road by a fence or natural border were defined as ‘roadside’ landscape type. Former cattle pastures were defined as ‘meadow’. The meadow areas were previously agricultural lease plots used for grazing but had been unused for this purpose for at least five years.

Study System

To examine the effects of foliage management on floral resources, I focused on five floral species that were present in the field sites that displayed a diverse array of life history characteristics and had known associations with the bumble bee *B. impatiens*. The selected species included four native wildflowers *Asclepias syriaca* (milkweed; Morse & Fritz 1983), *Monarda clinopodia* (basil balm; Whitten 1981), *Prunella vulgaris* (heal all; Kuriya, Hattori, Nagano & Itino 2015), and *Solidago rugosa* (wrinkle leaf goldenrod; Russo, DeBarros, Yang, Shea & Mortensen 2013) plus one naturalized non-native species, *Trifolium pratense* (red clover; Plowright & Hartling 1981). *A. syriaca* is a relatively large plant that reaches a height of 75 to 100 cm before flowering (Morse & Fritz 1983). Peak flowering occurs at mid-summer (Morse & Fritz 1983). *A. syriaca* has known associations with both diurnal and nocturnal pollinators, but pollination services come predominantly from diurnal species of which members of the genus *Bombus* are the most common (Morse & Fritz 1983). *M. clinopodia* is a perennial herb that flowers throughout late spring and summer. This plant usually reaches a height of 90-180 cm at bloom (NC Native Plant Society 2017). This species is known to have nectar foragers from the orders Hymenoptera (Families; Apidae, Halictidae, Andrenidae, Megachilidae), Lepidoptera (Families; Hesperriidae, Papilionidae, Nymphalidae, Noctuidae, Geometridae), Diptera (Family; Syrphidae), Coleoptera (Family; Cerambycidae), and Hemiptera (Family; Trochilidae) (Whitten 1981). The flower *P. vulgaris* is a perennial herb that blooms throughout late spring and summer (Kuriya et al. 2015, Lady Bird Johnson Wildflower Center 2015). This plant can bloom at a height as low as 5 cm and is common in many lawns (Lady Bird Johnson Wildflower Center

2015). *P. vulgaris* is predominantly pollinated by members of the genus *Bombus*. This plant shows a variety of corolla lengths and flower sizes that correlate with the tongue length and body size of bumble bees found alongside the flower (Kuriya et al. 2015). *S. rugosa* is an herbaceous plant that is common in many old growth meadows and reaches an average maximum height of approximately 90 cm (Sun & Frelich 2011). *Solidago* spp. overall are generalists for pollination, providing important food resources for a diverse array of insect visitors late in the summer and early fall after most other flowers have senesced (Ginsberg 1983). *T. pratense* is short lived perennial legume that flowers from late spring through the summer and has a stem length of between 21 and 51 cm when harvested for fodder (Sæbø & Mortensen 1995). *T. pratense* has been shown to enhance seed set when there are more genera of bee species present (Theodorou et al. 2017). Alternatively, it has also been observed that *Apis mellifera* and *Bombus spp.* are the primary pollinators of *T. pratense* and that short tongue bumble bees are considerably less effective at enhancing seed set than are long tongued bumble bees or the honey bee (Palmer-Jones, Foster & Clinch 1966).

Experimental Methods

Phenology plot establishment -- To test the effects of foliage management on abundance of plants important to *B. impatiens*, I established nine phenology plots each in the grassy areas located next to the former road (roadside habitats) and within open areas that were comprised of old fields allowed to revert to meadow. Each plot was 20 m^2 in area, and all plots with one exception (due to space) were arranged in a 2 m x 10 m rectangle; the other plot was 4 m x 5 m to accommodate space restrictions. Roadside plots (RPs) were generated as a random point along

the footpath within the permitted sampling area and a random distance from the footpath permitted by area restrictions. Due to area limitations, all roadside plots were oriented parallel to the path. Due to some locations along the path being unsuitable for study purposes (i.e., covered in trees, belonging to a private pasture, etc.) some locations along the path were unable to be selected if generated as a plot and a new random point was used to select the area. Meadow plots (MPs) were randomly generated as X and Y coordinates with a randomly generated orientation to north within the permitted study area. To mark the corners of my plots I used wooden stakes with flagging tape tied around them. I cleared fallen sticks, small brush, and hedges from my plots before data collection using a STIHL® FS 91 Professional Trimmer with brush cutter attachment or by hand.

Mowing regimes -- I randomly and evenly assigned the nine plots in each habitat to one of two foliage management regimes (mowed frequently or infrequently) or control (unmowed). Foliage management was implemented via mowing plots with a STIHL® FS 91 Professional Trimmer, which was also used to clear obstacles and create a footpath to access plots. Frequently managed plots were completely mowed to approximately two inches vertically parallel to the ground every three weeks during the experiment, whereas infrequently managed plots were cut to the same height, but only every sixth week. Mowing was always performed on Tuesdays and sampling flowers was performed on Mondays to avoid taking flower samples immediately after mowing treatments.

Inflorescence counts -- All plots were sampled weekly for abundance of inflorescences of the five focal plant species for the duration of the flowering period from May 7, 2018, through October 1, 2018. I constructed a 2 m x 5 m grid divided into 1 m x 1 m squares from bamboo

rods and nylon cord to grid off the plots for conducting inflorescence counts. During sampling, I placed the grid over the plot and counted the number of inflorescences of each focal flower species within each 1 m x 1 m quadrat. I then selected the inflorescence closest to the middle of the allotted quadrat and counted the number of flowers for future estimation of total flowers in each quadrat. For each weekly inventory, I recorded the date of sampling, the plot that the data were collected from, the portion of the plot (quadrat) being counted, the number of inflorescences of each flower species, and the number of flowers for one inflorescence of that flower species within each quadrat.

Statistical Analysis -- All statistical analyses were performed using R *o* (version 1.1.456). I first analyzed my data to ask whether applying mowing treatments impacted mean density of 1) inflorescences or 2) flowers (all plant species pooled) per square meter over time and whether this effect was consistent across roadside and meadow habitats. I determined mean densities for inflorescences andflowers separately by taking the average of quadrats within a plot on each date. I used a mixed effects repeated measures ANOVA with mean inflorescence density or mean flower density per square meter as the dependent variable. The factors 'Date', 'Mowing treatment', and 'Landscape' were considered as fixed factors in this model. The factor 'Plot' was considered a random factor in this model. The form of this statistical model was:

Mean inflorescences/square meter ~ Date, Plot, Mowing treatment, Landscape, Mowing treatment x Landscape

Mean flowers/square meter ~ Date, Plot, Mowing treatment, Landscape, Mowing treatment x Landscape

I analyzed my data with the same form of the mixed effects repeated measure ANOVA, but applied this analysis to mean 1) inflorescences or 2) flowers of each individual plant species to ask if the effects mowing treatment were consistent across target species. Like with the pooled species analysis, the mean inflorescence or flower density per square meter was the dependent variable and fixed and random factors were the same.

Lastly, I analyzed my data to ask if there was an effect of mowing treatment on the mean density of inflorescences or flowers of each individual plant species during the week of their peak abundance within the habitat type where they were most abundant as determined by a visualization of data as a graph. The species *A. syriaca* and *S. rugosa* were analyzed for abundance in the meadow habitat. All other species were analyzed based on their abundance within roadside habitat. I analyzed this using a one way ANOVA with the following models where mowing treatment was a fixed factor and mean inflorescence or flower density per square meter was the dependent variable:

Mean inflorescences/square meter ~ Mowing treatment

Mean flowers/square meter ~ Mowing treatment

Results

Results from mixed effects repeated measures ANOVA (floral species pooled; Fig. 1a, Table 1) showed that mean inflorescence density (flowering stalks) varied significantly over time (P <0.0001). Mowing had a significant impact on mean inflorescence abundance through time (P = <0.0001), with mowed plots, regardless of frequency, having fewer inflorescences than

unmowed plots (control). Mean inflorescence abundance did not vary among plots in the roadside vs the meadow ($P = 0.4643$), and the effect of mowing did not vary across habitat types ($P = 0.4684$). When floral display was quantified in terms mean flower density rather than inflorescences (Fig 1b, Table 2), the results showed that average flowers per m^2 varied by date ($P < 0.0001$), mowing treatment ($P < 0.0001$), habitat type ($P = 0.0038$), and the interaction between habitat type and mowing treatment ($P = 0.0010$).

When floral display was examined using mean inflorescence density for each individual species through time, mixed effects repeated measures ANOVA showed that mean inflorescence density varied significantly by date for only *S. rugosa* (Fig. 2e & 2f, Table 3; $P <0.0001$). Likewise, only *S. rugosa* showed a significant change in mean inflorescence density in response to mowing (Fig. 2e & 2f, Table 3; *P* 0.0001), with plots that were not mowed having higher inflorescence density than both mowed treatments. *S. rugosa* was the only species that showed a significant difference in mean inflorescence abundance due to habitat (Fig. 2, Table 3; $P = 0.0027$). The effect of mowing on *S. rugosa* inflorescence density varied among habitat types (Fig. 2, Table 3; $P = 0.0007$).

When floral display was quantified by flowers rather than inflorescences for each individual species the mixed effects repeated measures ANOVA showed that mean flower density varied over time for only *S. rugosa* (Fig. 3E & 3F, Table 4; $P <0.0001$). Only *S. rugosa* mean flower density varied among habitat type (Table 4; $P=0.0027$), with meadow habitat having greater floral density than roadside. *S. rugosa* flower density was also alone in showing significant change due to mowing (Table 4; $P =0.0001$), and the effect of mowing on flower density varied by habitat type for this species alone (Table 4; $P =0.0007$).

I found that when considering mean inflorescence density for each individual species only during the week of peak abundance that again only *S. rugosa* showed significant changes in abundance due to applying mowing treatments *Solidago rugosa* (Table 5; $P < 0.0001$). A similar pattern was observed when considering the mean density of flowers for individual species only at their peak abundance; only *S. rugosa* showed significant changes in flower abundance due to mowing treatment: *S. rugosa* (Table 6; $P < 0.0001$).

DISCUSSION

I performed this experiment with the intention of determining whether consistent mowing treatments influenced the density of inflorescences and/or flowers relevant to *Bombus impatiens*. I expected to find that mowing would be a detriment to flowers as a whole, but that low or fast growing plants might benefit or be less affected by the mowing process.

Quantifying floral resources over time (floral phenology) in two habitats showed that date was a highly significant factor across flower species as a pooled unit for both mean inflorescence density and mean flower density in both roadsides and meadows. These results are unsurprising, since individual flowers have a time of year they bloom according to factors like temperature and time exposed to sunlight (Tansey, Hadfield & Phillimore 2017). Other studies have shown that the timing of flower abundance is related to date and important for acknowledging periods of resource gaps for pollinators within agricultural ecosystems (Timberlake, Vaughan & Memmott 2019). I found that when considering the mean density of individual species that only *S. rugosa* showed a significant change in abundance through time. This suggests that the abundance of

species other than *S. rugosa* are relatively consistent throughout the flowering period, which results from the relative abundance of the species being so close to zero in the plots, and that *S. rugosa* has significant variation due to natural flowering period.

When assessing the effects of mowing, I found that when pooling counts of the five focal floral species, the mean densities of inflorescences and flowers important to *B. impatiens* were significantly influenced by the mowing treatment applied. Mowing, whether frequent or infrequent, lowered both the mean number of flowering stalks and the mean number of flowers available for providing resources for foraging worker bees collecting nectar and pollen to provision their home colonies. This is consistent with findings by Lerman et al. (2018) who found that the abundance of flowers within lawns in urban environments were considerably lower when mowing was implemented more frequently.

Analyses of individual species data showed that goldenrod, *S. rugosa*, was the most susceptible to changes in inflorescence and flower abundance through time due to mowing since it was the only species that reported a significant change due to mowing when considered individually. This is unsurprising since this plant is well over the maximum mowing height by the time it begins flowering, it was never found in a plot that was mowed, and in unmowed plots it was the most abundant plant across both meadow and roadside habitat when comparing peak abundance. This supports the findings of Bertoncini et al. (2012) who found that plant species vary greatly in their tolerance of mowing. *Solidago rugosa* showed a highly significant change in both mean inflorescence and flower abundance when mowing occurred, a highly significant difference in mean abundance between habitat types, and a highly significant effect of the interaction between habitat and mowing treatment. No other species showed significant changes

due to these factors. This first implies that implementing mowing treatments is detrimental to local abundances of *Solidago rugosa* since mowing treatment was a significant factor. It may also imply that the successional period of the habitat is important when determining abundance of *Solidago rugosa,* since the density of the plant was higher in the meadow habitat than in the roadside habitat; historically in my study area the roadside was mowed once per year, whereas the meadow had not been mowed in at least five years. My results also imply that mowing meadow habitat is more detrimental to local abundances of *Solidago rugosa* than is mowing roadside habitat since the interaction term between mowing and habitat was significant in my analysis for both inflorescence and flower density.

My peak date ANOVA analysis results show that the densities of inflorescences and flowers for *S. rugosa* during the week of peak abundance are negatively impacted by mowing. This predicts that the standing nectar resources that can be assimilated by *B. impatiens* at a given point in the season from a population of flowers can be reduced via mowing treatments. This detrimental effect due to mowing could lead to shortages of floral resources for supporting populations of *B. impatiens* since previous studies have found that resource availability during all portions of pollinator life cycle is important for maintaining pollinators (Timberlake et al. 2019). Empirical testing would be needed to conclusively assess impacts of mowing to pollinators.

Though rates are not available specific to *B. impatiens*, *Bombus* species overall require significant intake of resources to support a growing colony. For example, *Bombus agrorum* larvae are fed approximately 3-4 times per hour (Pendrel & Plowright 1981). Studies quantifying *Bombus terrestris* intake have shown that colonies took in an average of 58.49 grams of pollen and 677.87 milliliters of nectar under conditions where resource availability was unlimited,

leading colonies to produce an average of 96.56 workers. When resources were confined, colonies produced an average of 55.22 workers while consuming 22.96 grams of pollen and 428.8 ml of nectar (Schmid-Hempel & Schmid-Hempel 1998).

The rates at which *Bombus* larvae are fed depends on the caste and age of larvae and time since last feeding (Katayama 1973; Pendrel & Plowright 1981; Ribeiro, Velthius, Duchateau & van der Tweel 1999; Pereboom 2000; den Boer & Duchateau 2006), but generally as larvae age and grow, the frequency of feedings (and the need for collecting floral resources) increases (Pendrel & Plowright 1981). During caste development, queens develop for longer and thus require greater intake of resources compared to workers (Pereboom 2000). The more resources taken in, the more reproductives (queens and males) that are produced by each colony in the population (Schmid-Hempel & Schmid-Hempel 1998); barring effects of nest site limitation, the amount of resources available for collection should directly correlate with the number of queens that successfully establish new colonies the next season, i.e. the effective population size (N_e, the size of the breeding population).

In addition to mowing, habitat was a key factor influencing mean flower density (but not that of inflorescences), and that the effect of mowing varied by habitat. Meadow habitat produced more flowers in total throughout the season, largely due to the overwhelming abundance of *Solidago rugosa*. This result supports the finding of Warzecha, Diekotter, Wolters & Jauker (2018) who found that it is not necessarily the diversity of flowers that drives pollinators but the abundance of key plant species. This suggests that meadow habitat may be more vital to supporting bumble bees than roadside environments in regions where both habitats are present. However, it is worth noting that due to the earlier bloom time of the flowers (Fig.

1c), roadside areas are likely to contribute more towards supporting colonies of bees during the beginning of the season when food resources overall are more scarce. It is understood that within agricultural ecosystems that the presence of field margins and the proximity to natural environments that have floral resources for bees enhances the ability of wild pollinators to provide suitable ecosystem services to a variety of plants that depend on them (Carvalheiro et al. 2011). This suggests that both narrow patches of flowers, such as road margins, and larger swaths, such as meadows, provide resources that can enhance populations of wild pollinators. Other studies also suggest that unmanaged grasslands, such as old meadows, produce the most floral resources and draw the most visitors from wild pollinators including *Bombus spp.* when compared to habitat that is moderately managed, such as hedgerows, field margins (Lye, Park, Osborne, Holland & Goulson 2009), or roadside margins. There is also evidence that suggests that the size of quality floral patches is key to the conservation of bumble bee populations (Carvell et al. 2011). This also suggests that meadow habitat is more relevant to supporting *Bombus impatiens* since meadow habitat is likely to exist in much larger patches than roadside habitat by nature of roadside necessarily being on the perimeter of definable pathways.

While this study is valuable, it makes several assumptions. First, my five target species are representative of all resources relevant to *Bombus impatiens*. As a generalist foraging species with an expansive natural range (Russo et al. 2013; Looney, Strange, Freeman & Jennings. 2019) *B. impatiens* is reliant on more plant species than were present in my study sites. This suggests that quantifying the resources for *B. impatiens* within their entire range will require targeted studies in specific habitats in various locations where the bee is found. Additionally this study focuses on a single species of pollinator, but agricultural demand for pollination services

necessitates a diverse array of pollinators (Garibaldi et al. 2016) that may not be supported by the same wild plants. A proposed mechanism for the improvement of services by pollinator biodiversity is the morphological diversity of said pollinators. The functional diversity of bee groups is specifically known to have a positive correlation with the seed set of some wild and cultivated plants (Hoehn, Tscharntke, Tylianakis & Steffan-Dewenter 2008). This suggests that while the presence of *B. impatiens* is important, their persistence within environments will ultimately prove insufficient for supporting animal mediated pollination needs in the absence of other wild pollinators. Further, it is important to note that the variables measured to quantify floral display impacted the outcome of the test for habitat differences and the interaction term between habitat and mowing when considering each inflorescence or flower of any species as an equally weighted member of a population. This implies that the choice of variable used to assess outcomes may alter the findings of studies aimed at predicting and assessing land management impacts. Further research is needed to determine which outcome variable provides a more accurate assessment of resources available for pollinators under the different treatments.

This study is valuable for a number of reasons. Primary among them is that this study predicts the effects of anthropogenic land management on plant species relevant to a target pollinator. Anthropogenic land use in the form of agriculture and urban expansion tend to deplete the abundance of wild pollinators (Kremen, Williams & Thorp 2002). Since land use tends to grow alongside human populations, and humanity is still increasing in number, it is estimated that suitable habitat for wild pollinators will continue to decline (Winfree et al. 2011). This being the case it is important for humanity to understand the ways that we can best mitigate the damage that comes about through our growth and to find methods for supporting both environments that

provide suitable resources for pollinators and provide sustainable agriculture for supporting humanity. The information provided by this study is useful when trying to predict the changes in resources that are relevant to populations of *B. impatiens* and defining land management strategies that could best mitigate the detrimental effects of human expansion. This study could be expanded upon further by including other habitat types, like urban lawns, to further determine the effects of anthropogenic land use on flower resource availability. Including a wider sampling area could also provide valuable information as other plant species, such as the white clover *Trifolium repens*, relevant to *B. impatiens* exist outside of the permitted sampling area in considerable abundance. Additionally, performing floristic studies on all plant species found within sampled environments, instead of a subset, and their response to mowing could provide information about potential impacts of mowing on pollinator species other than *B. impatiens*.

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TABLES

Table 1: Mixed effects repeated measures ANOVA testing for inflorescences. Flower species pooled and weighted equally.

	numDF	denDF	F-value	p-value
(Intercept)	1	289	14.835	0.001
Date	17	289	2.256	0.003
Mowing	2	12	13.758	<0.001
Habitat	1	12	0.571	0.464
Mowing:Habitat	2	12	0.809	0.468

Table 2: Mixed effects repeated measures ANOVA testing for flowers. Species pooled and weighted equally.

	numDF	denDF	F-value	*p*-value
(Intercept)	1	289	30.365	<0.001
Date	17	289	17.905	<0.001
Mowing	2	12	11.901	<0.001
Habitat	1	12	0.297	0.004
Mowing:Habitat	2	12	0.495	0.001

Table 3: Mixed effects repeated measures ANOVA testing for inflorescence. Analysis performed individually by species.

	numDF	denDF	F-value	p-value
Asclepias syriaca				
(Intercept)	1	289	1.697	0.194
Date	17	289	1.060	0.393
Mowing	2	12	1.697	0.224
Habitat	1	12	1.697	0.217
Mowing:Habitat	2	12	1.697	0.224
Monarda clinopodia				
(Intercept)	1	289	1.153	0.283
Date	17	289	1.188	0.272
Mowing	2	12	1.153	0.348
Habitat	1	12	1.153	0.303
Mowing:Habitat	2	12	1.153	0.348
Prunella vulgaris				
(Intercept)	1	289	1.644	0.200
Date	17	289	1.055	0.399
Mowing	2	12	1.033	0.386
Habitat	1	12	1.644	0.224
Mowing:Habitat	2	12	1.033	0.385
Trifolium pratense				
(Intercept)	1	289	1.016	0.314

Date	17	289	1.040	0.415
Mowing	2	12	0.992	0.399
Habitat	1	12	1.016	0.333
Mowing:Habitat	2	12	0.992	0.399
Solidago rugosa				
(Intercept)	1	289	80.222	<0.001
Date	17	289	47.381	<0.001
Mowing	2	12	80.053	<0.001
Habitat	1	12	46.577	0.003
Mowing:Habitat	2	12	46.706	0.001

Table 4: Mixed effects repeated measures ANOVA testing for flowers. Analysis performed individually by species.

	numDF	denDF	F-value	p-value
Asclepias syriaca				
(Intercept)	1	289	1.855	0.174
Date	17	289	1.106	0.347
Mowing	2	12	1.855	0.199
Habitat	1	12	1.855	0.198
Mowing:Habitat	2	12	1.855	0.199
Monarda clinopodia				
(Intercept)	1	289	1.105	0.287
Date	17	289	1.145	<0.001
Mowing	2	12	1.105	0.353
Habitat	1	12	1.105	0.307
Mowing:Habitat	2	12	1.105	0.353
Prunella vulgaris				
(Intercept)	1	289	1.740	0.189
Date	17	289	1.093	<0.001
Mowing	2	12	1.152	0.409
Habitat	1	12	1.740	0.213
Mowing:Habitat	2	12	1.152	0.409
Trifolium pratense				
(Intercept)	1	289	1.010	0.316
Date	17	289	1.027	0.429
Mowing	2	12	0.995	0.398

Habitat	1	12	1.010	0.335
Mowing:Habitat	2	12	0.995	0.398
Solidago rugosa				
(Intercept)	1	289	23.567	<0.001
Date	17	289	4.039	<0.001
Mowing	2	12	23.559	<0.001
Habitat	1	12	14.225	0.003
Mowing:Habitat	2	12	14.232	<0.001

Table 5: One way ANOVA showing the effects of mowing on peak inflorescence abundance for focal species.

	DF	Sum Sq	Mean sq	F-value	Pr(>F)
Asclepias syriaca					
Mowing	2	4.44	2.22	4.13	0.018
Residuals	177	95.33	0.54		
Monarda clinopodia					
Mowing	2	13.61	6.81	9.67	<0.001
Residuals	177	124.58	0.70		
Prunella vulgaris					
Mowing	2	132.01	66.01	14.34	<0.001
Residuals	177	814.98	4.60		
Trifolium pratense					
Mowing	2	23.01	11.51	8.94	<0.001
Residuals	177	227.72	1.29		
Solidago rugosa					
Mowing	2	1299.60	649.82	174.12	<0.001
Residuals	177	660.65	3.71		

Table 6: One way ANOVA showing the effects of mowing on peak flower abundance for focal species.

	DF	Sum Sq	Mean sq	F-value	Pr(>F)
Asclepias syriaca					
Mowing	2	18091	9045	5.1	<0.001
Residuals	177	313162	1769		
Monarda clinopodia					
Mowing	2	2465	1233	7.5	<0.001
Residuals	177	29128	165		
Prunella vulgaris					
Mowing	2	6469	3234	10.1	<0.001
Residuals	177	815	5		
Trifolium pratense					
Mowing	2	10430	5215	7.9	<0.001
Residuals	177	117179	662		
Solidago rugosa					
Mowing	2	5811013	2905506	103.6	<0.001
Residuals	177	4962052	28034		

FIGURES

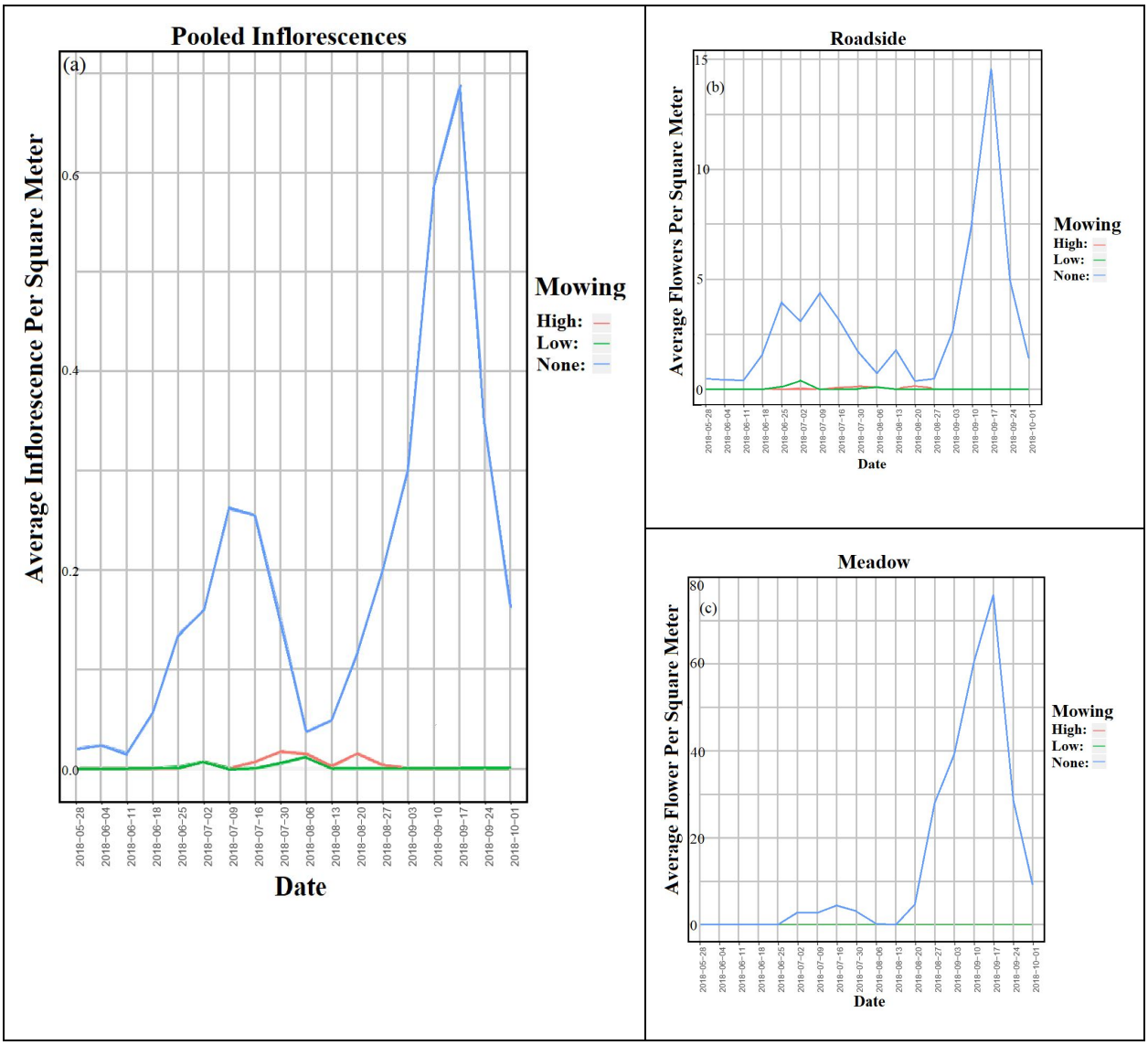
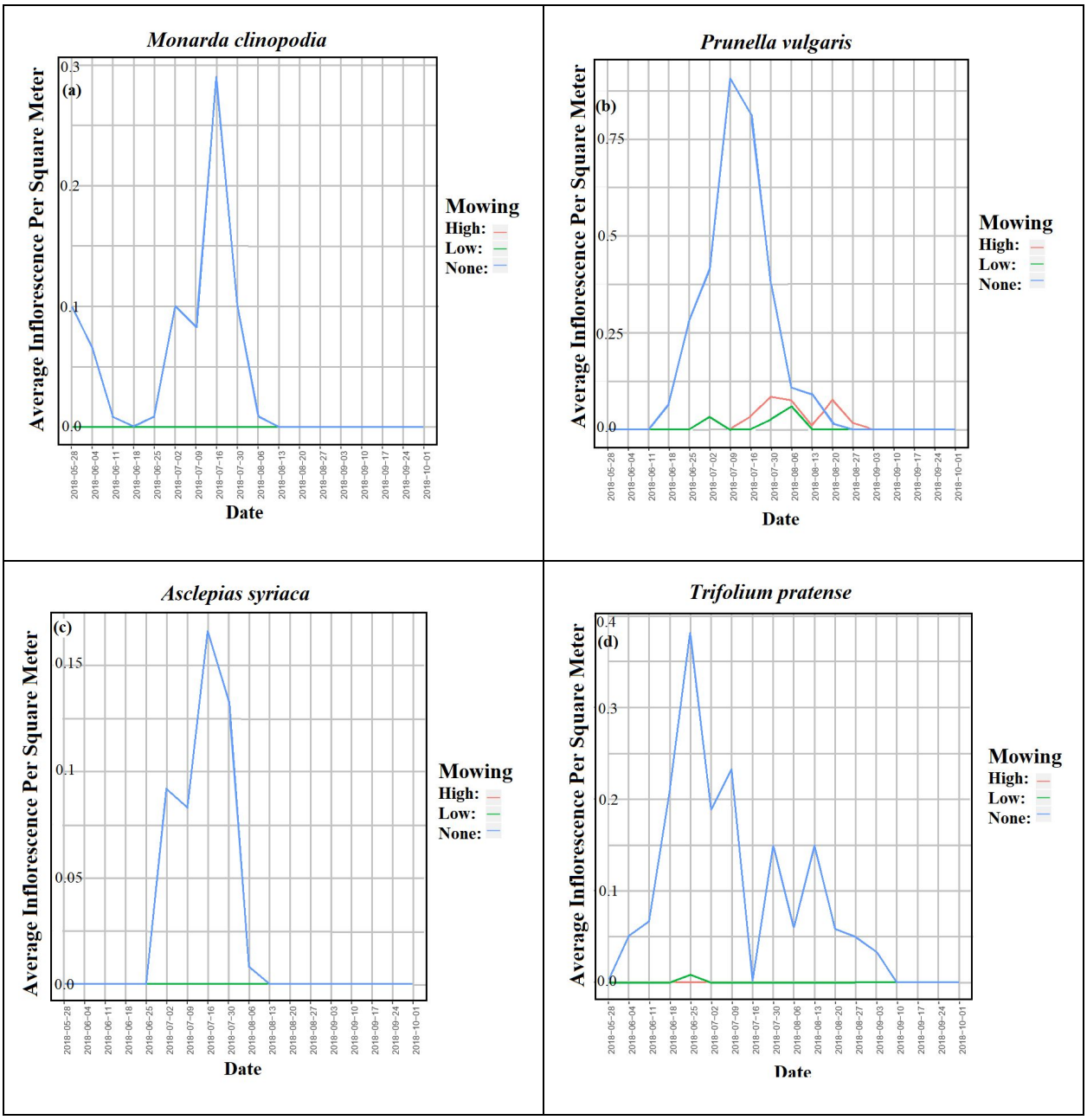


Figure 1: A) Inflorescence density in pooled habitat B) flower density in roadside habitat type and C) flower density in meadow habitat through time (all floral species pooled) under experimental mowing treatment regimes.


Monarda clinopodia
(a)
Average Inflorescence Per Square Meter
0.3
0.2
0.1
0.0
Date
Mowing
High:
Low:
None:
Prunella vulgaris
(b)
0.75
0.5
0.25
Asclepias syriaca
(c)
0.15
0.05
Trifolium pratense
(d)
0.4
2018-05-28
2018-06-04
2018-06-11
2018-06-18
2018-06-25
2018-07-02
2018-07-09
2018-07-16
2018-07-30
2018-08-06
2018-08-13
2018-08-20
2018-08-27
2018-09-03
2018-09-10
2018-09-17
2018-09-24
2018-10-01

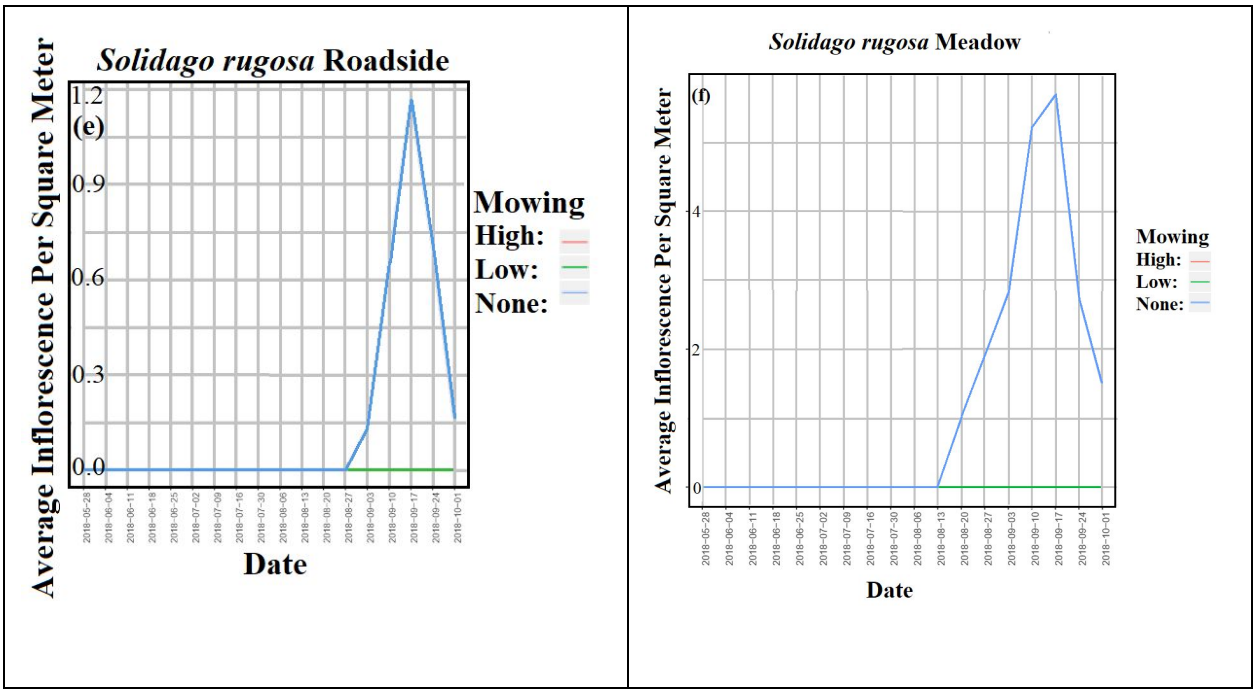
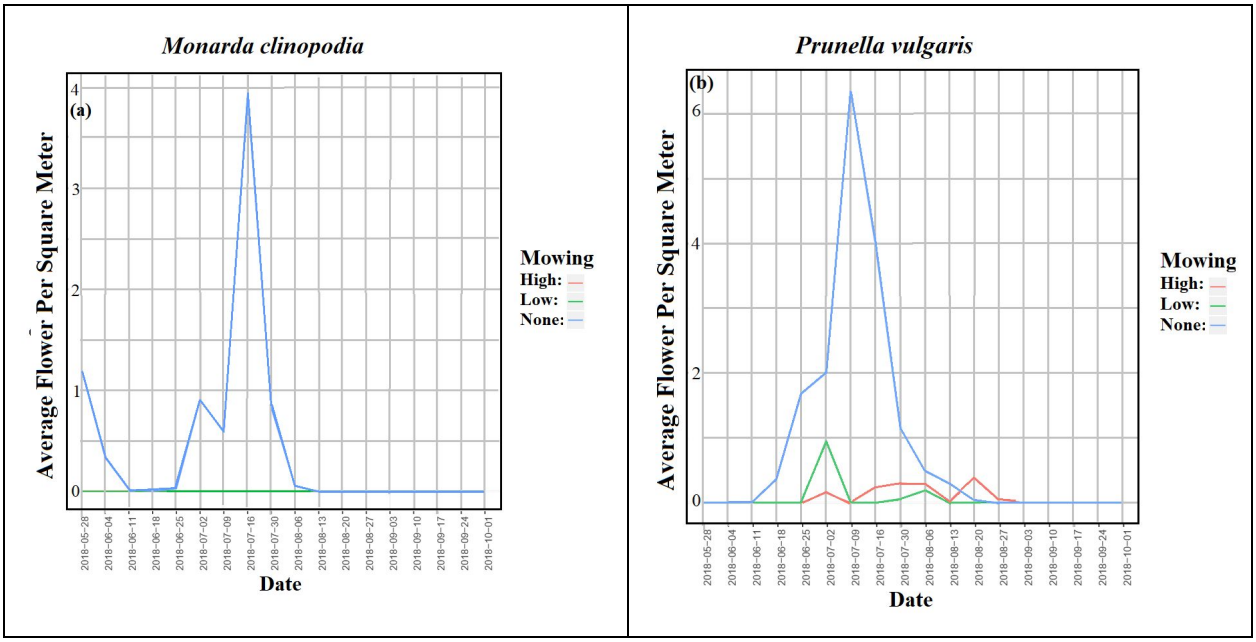


Figure 2: Inflorescence density for A) *Monarda clinopodia* B) *Prunella vulgaris* C) *Asclepias syriaca* D) *Trifolium pratense* E) *Solidago rugosa* in roadside habitat and F) *Solidago rugosa* in meadow habitat.



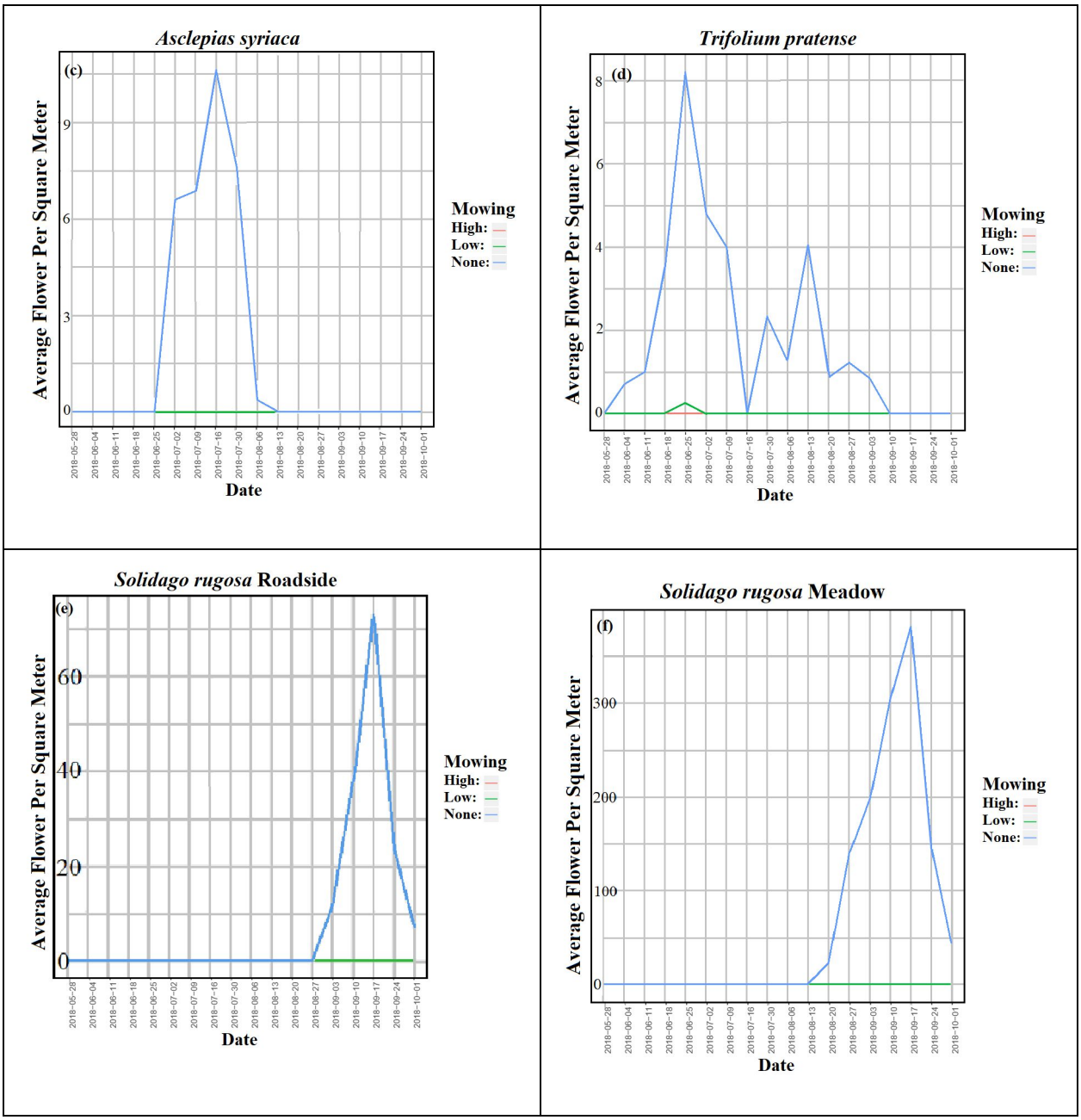
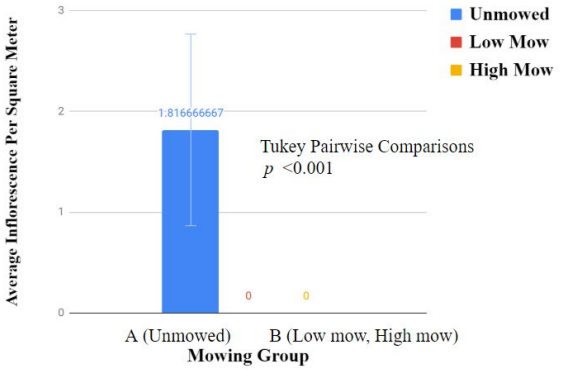
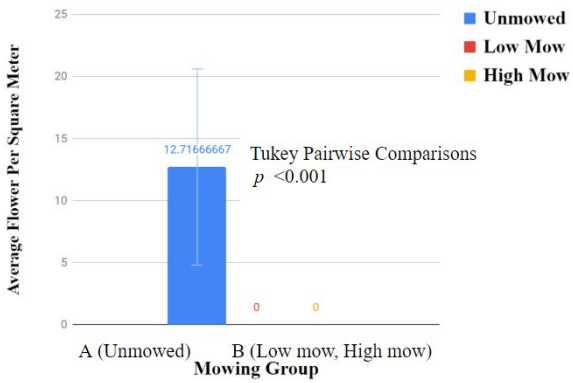
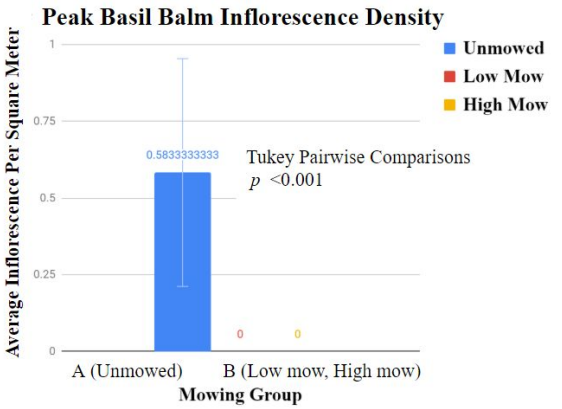
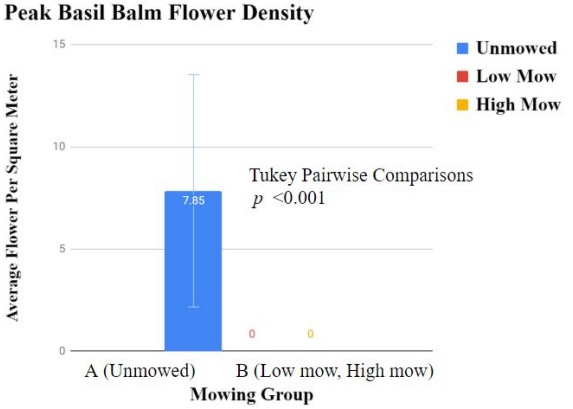


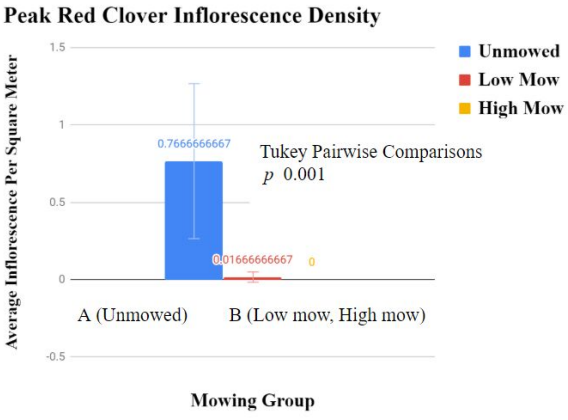
Figure 3: Flower density for A) *Monarda clinopodia* B) *Prunella vulgaris* C) *Asclepias syriaca* D) *Trifolium pratense* E) *Solidago rugosa* in roadside habitat and F) *Solidago rugosa* in meadow habitat.

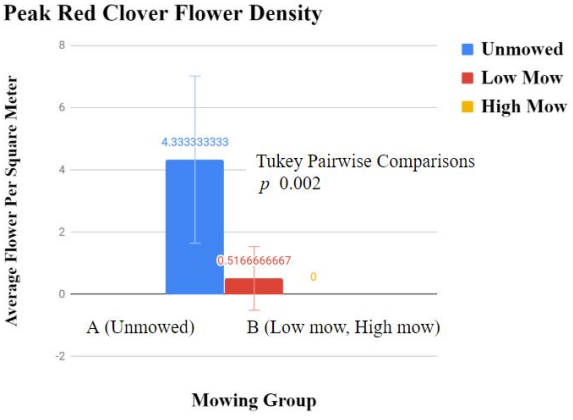

Peak Heal All Inflorescence Density
Average Inflorescence Per Square Meter
3
2
1
0
1.816666667
0
0
Unmowed
Low Mow
High Mow
Tukey Pairwise Comparisons
p <0.001
A (Unmowed)
B (Low mow, High mow)
Mowing Group


Peak Heal All Flower Density
Average Flower Per Square Meter
25
20
15
10
5
0
12.71666667
0
0
Unmowed
Low Mow
High Mow
Tukey Pairwise Comparisons
p <0.001
A (Unmowed)
B (Low mow, High mow)
Mowing Group


Peak Basil Balm Inflorescence Density
Average Inflorescence Per Square Meter
1
0.75
0.5
0.25
0
0.5833333333
0
0
Unmowed
Low Mow
High Mow
Tukey Pairwise Comparisons
p <0.001
A (Unmowed)
B (Low mow, High mow)
Mowing Group


Peak Basil Balm Flower Density
Average Flower Per Square Meter
15
10
5
0
7.85
0
0
Unmowed
Low Mow
High Mow
Tukey Pairwise Comparisons
p <0.001
A (Unmowed)
B (Low mow, High mow)
Mowing Group


Peak Red Clover Inflorescence Density
Average Inflorescence Per Square Meter
1.5
1
0.5
0
-0.5
0.7666666667
0.01666666667
0
Unmowed
Low Mow
High Mow
Tukey Pairwise Comparisons
p 0.001
A (Unmowed)
B (Low mow, High mow)
Mowing Group


Peak Red Clover Flower Density
Average Flower Per Square Meter
8
6
4
2
0
-2
4.333333333
0.5166666667
0
Unmowed
Low Mow
High Mow
Tukey Pairwise Comparisons
p 0.002
A (Unmowed)
B (Low mow, High mow)
Mowing Group

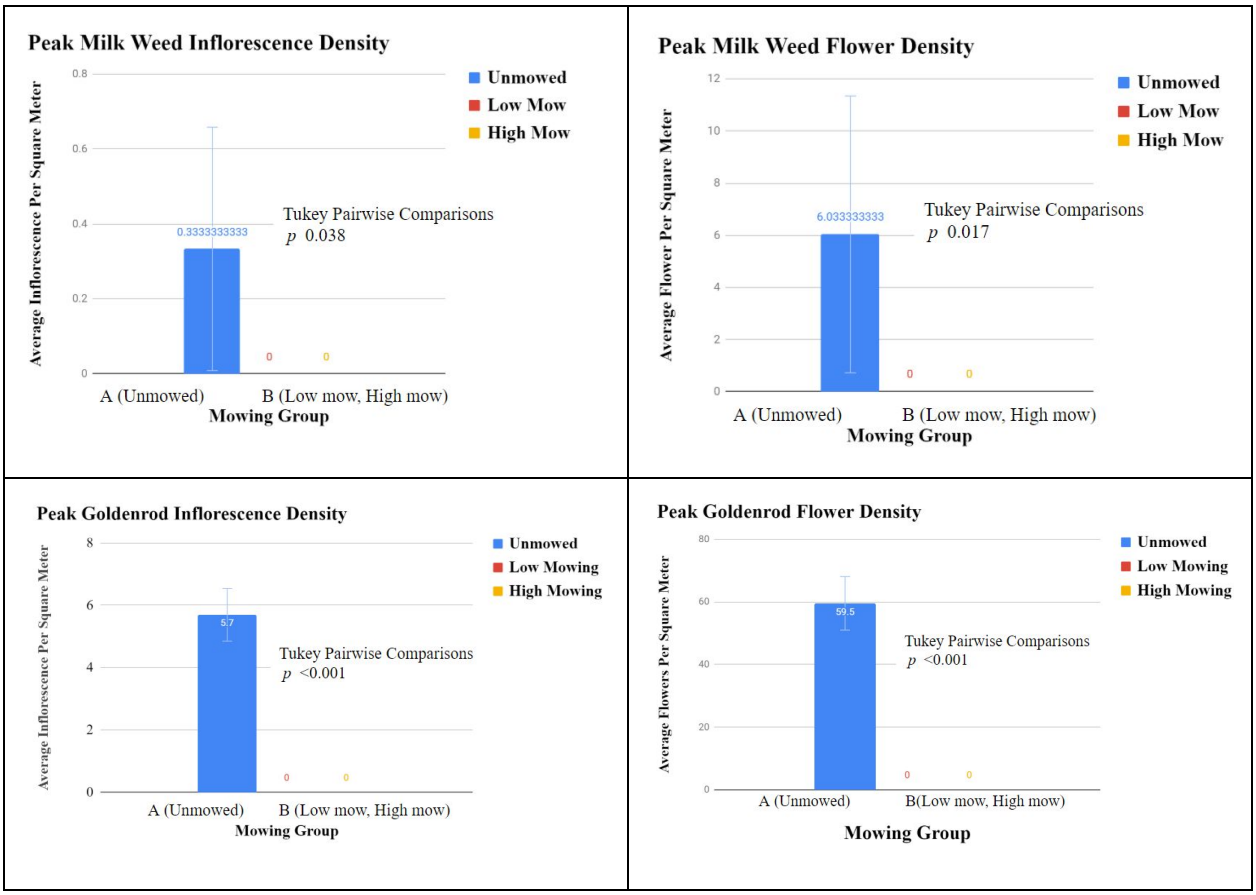


Figure 4: Pairwise peak flower and inflorescence abundance comparison for target species.

CHAPTER III

Modeling the Effects of Foliage Management on *Bombus impatiens*

ABSTRACT

The purpose of this model was to demonstrate the potential effects of mowing roadside and meadow habitat on populations of the bumble bee species *Bombus impatiens*. This model uses a combination of floral data I collected and parameters defining the life history of the bee derived from the literature to track changes in nectar resources produced in an explicit, sixteen patch landscape and to track changes in bumble bee populations that are dependent on these resources. This model demonstrates that mowing can have an indirect impact on the abundance of *B. impatiens* within the areas that are mowed through deprivation of floral resources.

Through performing these models I found that the management practices of large meadow areas has the greatest potential to impact flower abundance, and thus populations of pollinators. I also found that management of roadside habitat contributes to the ability of pollinators to assimilate appropriate resources.

This model provides the means to make recommendations about the ideal management practices for supporting the bumble bee *B. impatiens* that could be implemented on grassy areas found next to or near roadways.

INTRODUCTION

Ecological modeling techniques have been used to estimate populations of bumble bees in a variety of ways and with varying techniques. One study modeled the effects of source sink dynamics of bumble bee populations within a heterogeneous landscape on a large scale and with a long term timeframe. This study used a spacial matrix coupled with linear equations that compile annual populations using in season parameters (Iles, Williams & Crone 2018). The previous study derived equations for inner season dynamics from another study that modeled the effects of land use and floral resources on colony grown and queen production for *Bombus vosnesenskii* within a heterogeneous landscape. This model included a sensitivity term for colony growth based on resources availability that was the most determining of the model, demonstrating how necessary it is to focus efforts on quantifying within colony dynamics (Crone & Williams 2016). Another study has proposed the use of delay differential equations to represent bumble bee life history. This study demonstrates that delay differential equations allow the ability to quantify the allocation of resources to different tasks within a colony at different times, such as a queen ending foraging and devoting resources to worker production (Banks, Bommarco, Rundlof & Tillman 2017). There has also been a model for bumble bees that demonstrates the interactions of a parasite with its host bee using linear equations to determine the spatio-temporal relationship. This study demonstrated the need for long term data sets in developing appropriate models for subtle ecological processes (Antonovics & Edwards 2011). Populations of bumble bees have been modeled using series of discrete equations applied to a

theoretical landscape, where individual facets of life history are represented via different equations (e.g. in agricultural landscapes, Haussler, Sahlin, Baey, Smith & Clough 2017). This modeling method is of particular use when isolating factors that influence populations and is well established for a variety of species and ecological interactions (Keitt 2009; Liu, Bai & Jim 2017). Agent-based (individual-based) models have also been used; these systems also use a theoretical landscape but allow individual colonies and bees to behave uniquely according to their surroundings and individual behavior rather than having equations represent whole populations. Agent-based models are extremely powerful when quantifying bumble bee behavior and the effects of multiple stressors that might exist within an explicit landscape. They have been shown to relate well to empirical data for foraging behavior, colony growth, reproduction, and estimated nest densities (Becher et al. 2018).

Like with all representative models, the life history of the bumble bee must be taken into consideration when creating a representative model. The first is that bumble bees are central place foragers, requiring that all collected resources be returned to the home location for assimilation; resources that are closer to the colonies of bees are more efficiently collected (Darvill, Knight & Goulson 2009). In addition, colony-specific foraging distances can be altered due to resource availability within the landscape (Carvell et al. 2011). This can make determining the best way to model bumble bee foraging difficult. Further complexity arises from the phenology of *Bombus* nests. At the beginning of flowering season only workerless queens exist and resources are allocated to producing workers; later in the season queens cease foraging and workers assimilate resources for the queen in order to produce new reproductives (Hendriksma, Toth & Shafir 2019). This can be appropriately represented in a model by having

two equations for resource collection at temporally explicit points (Haussler et al. 2017). Because the flower phenology data I collected gave insight into bloom time I selected the Haussler model for use in conjunction with this data because the model allowed for this two step resource collection at different times in the flowering season.

In addition to representing basic life history traits of focal populations, ecological models often include other factors that impact the growth of populations over time. Density dependent factors (DDFs) show a proportionate change in their capacity to influence populations as the size of the focal population changes. Density independent factors (DIFs) tend to affect populations in a more proportionally equivalent way across a gradient of population sizes. Density dependence is commonly understood as intraspecific competition, which confines population sizes because the niche being occupied by the species has limited resources. Because members of the same species, and sometimes multiple species, compete for these limited resources, the availability of resources is a DDF (Ehrlen & Morris 2015). Density independence is commonly associated with some sort of unavoidable cataclysmic event that has predictable direct negative effects on populations within a given area, such as a fire or flood. Alternatively DIFs can be the result of human interference, as in the case of agricultural pesticide use (Hladik, Vandever & Smalling 2016). The relative degree to which DDFs and DIFs impact population dynamics is still unclear but is likely related to the life history traits possessed by the focal species (Henle, Davies, Kleyer, Margules & Settele 2004).

The goal of this project was to model the population dynamics of the bumble bee *Bombus impatiens* and examine the effects of foliage management on the availability of floral resources

relevant to the bees through simulation. I used a series of discrete equations (Haussler et al. 2017) to model *B. impatiens* life history within an explicit landscape. I then used the model to simulate the impacts of different frequency of vegetation mowing of roadsides and meadows on colony resource assimilation, worker production, and colony density within the landscape. The output of this model was intended to show how resource availability limits the abundance of *B. impatiens*. I also used this model to predict the ideal position within a landscape for colonies of *B. impatiens* to have the greatest chance of persistence.

MATERIALS AND METHODS

Bumble bees, like all organisms, have specific life history characteristics that can constrain the population size. One factor that constrains their population is the availability of suitable nesting habitat. Bumble bees are cavity dwelling bees, and as such require pre-made structures to establish a colony. These structures may be hollow sections of trees, man-made structures such as sheds or birdhouses, or most commonly abandoned subterranean mammal burrows (Gaston, Smith, Thompson & Warren 2005). The total number of these suitable structures that exist in a given area limits how many colonies of bumble bees can exist in that area. If there are a greater number of queen bees searching for nesting sites it is more difficult for each individual to successfully find a site and establish a colony due to intraspecific competition. Thus, nesting resources for bumble bees acts as a DDF. A second species trait that confines populations of bumble bees is their dependence on floral resources. Bumble bees require carbohydrate input from floral nectar and protein input from pollen in order to persist. Quantities of relevant floral resources are limited by the number of flowers in a given area and by how

effectively the relevant flowers produce said resources (Heil 2011). Because the total resources that are available to bees is finite, inter- and intraspecific competition for resources is likely. As with the case of suitable nests, the likelihood of collecting a suitable amount of quality resources is diminished for each individual in the population as the total size of the bee population grows or as the total amount of resources declines, making floral resources a DDF (Kremen, Williams & Thorp 2002).

There are DIFs that can influence populations of bumble bees, as well. For instance, temperature can impact how efficiently bumble bees are able to forage for resources, which can in turn impact the overall ability of a colony to produce viable reproductive individuals. This occurs due to a requirement by the bumble bee to regulate the temperature of the thoracic muscles that power the wings by utilizing some of the resources that are gathered during foraging. These muscles must meet the minimum threshold temperature in order to produce sufficient force to allow the bumble bee to take and maintain flight, therefore it is possible that uncharacteristically cold weather during a bumble bee season could impact the overall net fecundity by decreasing the overall net resource assimilation (Heinrich 1975). Each individual bee would be impacted in a similar manner by cold weather no matter what the overall population density in the area is, thus making seasonal thermoregulation a DIF. Another circumstance that can drastically influence bumble bee populations is exposure to pesticides. Common agricultural practices include the use of high quantities of potent insecticides to deter herbivory by pest species. This practice can have unintended consequences for bumble bees that visit plants that were treated with the toxin. Direct mortality due to pesticide exposure can act in a density independent way because the gross mass of chemical toxins that are supplied to the

area vastly exceeds the total amount of toxins that would be required to eliminate all individuals should they be directly exposed and thus has the capacity to affect every individual bee in the same manner, regardless of density (Hladik et al. 2016).

There are certain aspects of the life history of bumble bees that seem to act as both DDFs and DIFs. The behavior of individual worker bees contributes to their ability to persist and contribute to procreation. Each activity that the individual performs presumably has an average mortality rate associated with it and an average benefit garnering rate, even if the rates are unknown. Inadvertently spending more time performing activities that are higher risk or lower reward could increase the likelihood of dying for that individual or become such a detriment to efficiency that fecundity is reduced. This suggests that the dynamics a population can be influenced by foraging behavioral trends. There are components of foraging behavior that operate in a density dependent manner, especially when densities of multiple species are considered. Bumble bees, and many other species that gather food resources, have behavioral patterns that help dictate appropriate times and places to forage. The density of flowers in an area can impact the decisions that pollinators make. Bumble bees, because they have limited ocular resolution, use a strategy called 'green contrast' to appropriately locate and identify patches of resources from afar. This process essentially allows the bee to compare the target area and its surroundings based on how green they are. Patches of flowers that are less dense will appear more green and will consequently be visited at a lower rate (Chittka & Raine 2006). Because the density of the flowers is influencing the behavioral pattern of the bees and the bees are competing for these flowers, foraging behavior can be influenced in a density dependent way. There are DIFs that influence foraging behavior as well. For example, bumble bees have an

aversion to foraging in the rain. The density of bumble bees in the area will not play a role in the suppressive ability of rain on foraging, but will instead be dictated by the individual bees ability to cope with the inclement weather. One proposed mechanism to explain this phenomenon is that a wet bee weighs more and thus requires more energy to stay aloft (Heinrich 1975). This would fit within the concept of density independence in that every bee would be inhibited roughly equivalently by being soaked. An alternative hypothesis for the tendency of bees to avoid rain is that visibility is impaired during rain events, and so foraging efficiency is decreased due to an increase in searching time (Chittka & Raine 2006). Whatever it is about the rain that represses foraging rates, it does not appear to dappen due to the number of pollinators in the area. This suggests that there are both DDFs and DIFs that can influence foraging behavior for bumble bees.

Simulated Environment

I modeled a single landscape found in Watauga County, North Carolina (Fig. 1). The landscape was 2 x 2 kilometers in size and was located along The Blue Ridge Parkway in Julian Price park and included a mix of forested area, meadow grasslands, roadside grasslands, and water. The landscape was broken into 16 cells arranged in a 4 x 4 pattern, making the size of each cell 500 x 500 meters. This model landscape was simulated for five years as a projection with outputs for each landscape cell showing resources collected during early summer, resources collected during late summer, workers produced in one season, and new queens produced that successfully nest within the landscape. This model was repeated under four theoretical mowing regimes with different empirical data sets to examine the consequences of different land

management strategies. Specifically, the model looked at how populations of *B. impatiens* respond to an environment: (1) completely devoid of mowing, (2) where only roadsides are mowed, (3) where only meadows are mowed, and (4) where mowing is applied to both roadsides and meadows.

Each of these situations was simulated three times with iterations out to five years. The model developed isolated a few key factors for interpretation within the readout: (1) total colony number overall, (2) colony number by landscape cell, (3) flower resources produced overall, and (4) flower resources produced by cell. I developed the code and theory for representing a landscape as matrices in this way and used this method alongside equations derived from the literature.

Landscape Cell Scores

To develop my model I modified an existing model found in Haussler et al. (2017). Haussler used cells within the theoretical landscape that represented 25 x 25 meter sections of a 10 square kilometer explicit landscape. In my model, landscape size in total was 4 square kilometers and each cell of my landscape was representative of a 500 x 500 meter section.

As in the Haussler model each of the cells in my landscape had a nesting score and a resource score assigned to them. In the original model the nesting scores were variable based on the type of landscape cover but my model assumed that all cells in a landscape were equal in nesting quality. This assumption was made for the purpose of isolating the effects of changes in resource abundance, which was my primary focus.

The resource scores for landscape cells in Haussler et al. were based on the habitat cover type of the area and the predicted floral quality of the area based on that cover type as derived from the literature. Each cell in the model by Haussler et al. was defined by a single habitat type. My model operated on a similar idea for assigning resource score in that each of my cells was given a predictive resource score based on flower abundance and quality. I assigned a value to each landscape cell based on the percent of habitat types found within the cell instead of assigning a single habitat type to each cell and basing the score from this as was done in the Haussler model. My model was also distinct because it was based on floral abundance and nectar data that I collected from five target flower species known to be important in the field of *B. impatiens* in areas found within the modeled landscape instead of deriving these values from literature. The parameters I used for estimating populations of bumble bees is based on the Haussler model which derived specific parameters from empirical studies on bumble bee abundance within agricultural landscapes.

Bombus impatiens Population Modeling

I used data from floral phenology studies (Chapter 1) and from nectar analysis (Appendix I) of five focal flower species to quantify the relative changes in nectar resources that occurred due to implementing mowing treatments, and potential impacts that these changes could have on the population dynamics of *B. impatiens*. The model from Haussler et al. (2017) was used to determine relative changes in population size and to quantify differences in pollinator ecosystem services from *Bombus terrestris*, which is a ground dwelling bumble bee like *Bombus impatiens*, within an agricultural landscape. My model operates on the same equations used by Haussler et

al. for estimating relative changes in resource assimilation and population changes, but provides slightly different insights since my model does not focus on the benefit that crops might yield from increased visitation by bumble bees. My model focuses specifically on quantifying the ability of *Bombus impatiens* to garner resources and reproduce under specific foliage management regimes. This model also provides evidence about what location within a landscape is most beneficial for a colony of *Bombus impatiens* to exist within since part of the output displays the cells that garner the most resources.

The first equation to iterate this model is for visitation rate by *Bombus impatiens* from each individual cell to every other cell within the explicit landscape. This equation is of primary interest when determining the ability of the bee to provide pollination services. This is calculated using the equation:

$$VR_{j\to i}^{k} = X_{k,j}\frac{F_{i,k}e^{-d_{ij}/\beta}}{\sum_{q=1}^{n} F_{q,k}e^{-d_{qj}/\beta}}\rho_{F}^{d_{ij}}$$

Where VR is the visitation rate during time period k for bees from cell j to cell i, X is the total number of bees able to forage that exist in cell j during time period k, F is the abundance of floral resources available in a given cell, ρ_F is the survival rate of foraging bees per distance traveled within the landscape, d_{ij} is the euclidean distance between cells i and j. The equation weights each cell for attractiveness based on the resources in the individual cell of interest (i.e., F_i represents resources in cell i) compared to the total available resources across the entire landscape which is represented by the summation of all resource scores (i.e., sum of F_q). This equation assumes that all colonies have perfect information about where resources are located and the relative difficulty of acquiring these resources. It also assumes that the amount of nectar

resources available for assimilation and the distance of the resources from the colony are the only influences for visitation rates of *Bombus impatiens*.

The second equation used in one season of this model is used to determine the amount of resources that are taken into a single colony of *Bombus impatiens* located in each individual cell.

$$R_{k,i} = \frac{X_{k,i}}{N_i} \sum_{j=1}^{n} F_{k,j} \frac{e^{-d_{i,j}/\beta}}{\sum e^{-d_{i,j}/\beta}}$$

Where $R_{k,i}$ is the amount of nectar resources taken into cell i during time period k. $X_{k,i}$ is the proportion of *B. impatiens* individuals that are from cell i that are foraging during time period k. N_i is the total number of colonies that exist within cell i. $F_{k,j}$ is the resource score of cell j during time period k. $d_{i,j}$ is the geometric distance between cells i and j. β is the mean foraging distance assigned to *B. impatiens*. This equation assumes that all individuals within bumble bee colonies behave the same way, that all individuals within and across colonies are equally able to collect resources, and that colonies existing in the same cell will take in exactly the same amount of resources.

The third equation form used to iterate a single season of this model is for tracking populations of workers produced during the first portion of the flowering season and for tracking the production of queens during the later portion of the flowering season.

$$W_i = Q_i \cdot w_{max} \cdot G(R_{1,i}, a_w, b_w)_{\text{season}}$$

$$Q_{E,i} = Q_i \cdot q_{max} \cdot G(R_{2,i}, a_Q, b_Q)$$

Where W_i is the number of workers produced in landscape cell i during the first period of the flowering season, Q_i is the number of colonies that exist in landscape cell i, W_{max} is the maximum number of workers that can be produced by a single colony, G(-,a,b) is a cumulative log normal distribution with mean a and variance b, $R_{1,i}$ is the resources collected score of cell i for the first period of the flowering season, a_w is the mean number of workers produced by a colony of *Bombus impatiens*, b_w is the variance of number of workers produced by colonies of *Bombus impatiens* as it relates to changes in production due to changes in assimilated resources, $Q_{E,i}$ is the number of queens produced in landscape cell i during the later portion of the flowering season, q_{max} is the maximum number of queens that can be produced by a single colony of *Bombus impatiens*, $R_{2,i}$ is the resources assimilated score for landscape cell i during the second portion of the flowering season, a_Q is the mean number of queens produced by a colony of *Bombus impatiens*, and b_Q is the variance of the number of queens that can be produced by a colony of *Bombus impatiens* as it relates to changes in production due to changes in assimilated resources.

The final equation used in a single iteration of this ecological model is for determining how new queens that are produced within landscape cell will disperse and establish new colonies in the subsequent year.

$$Q_{E,j\to i} = Q_{E,j}\frac{Q_i e^{-d_{i,j}/\beta_d}}{\sum_{q=1}^{n} Q_q e^{-d_{k,j}/\beta_d}} P_N^{d_{i,j}}$$

Where $Q_{E,j\to i}$ is the number of queens from cell j that successfully nest in cell i during the subsequent year, $Q_{E,j}$ is the number of queens produced in cell j, Q_j is the number of established colonies in cell j, $d_{i,j}$ has already been defined as the geometric distance between cells i and j, β_d

is the dispersal distance of queens when seeking nesting sites, and P_N is the survival rate per distance traveled across the landscape for dispersing queens. This portion of the model assumes that queens mate and overwinter in the cell in which they are produced and disperse to the cell in which they will nest in the early spring.

I used values for the parameters of this model based on the original version of this model when appropriate (Haussler et al. 2017). The parameter values not derived from Haussler et al. were arbitrarily assigned for simplifying purposes and are marked in Table 1 as (a). It is worth noting that actual values for these arbitrarily assigned values exist, but quantifying these parameters in field studies is extremely difficult and no appropriate values were located within the literature. These values are also likely to differ due to a variety of biotic and abiotic factors and would need to be determined experimentally for every landscape that is modeled using these equation forms.

RESULTS

I compiled outputs from the ecological projection model with variations based on nectar availability due to mowing implementation. The primary output that I tracked was the colonization of patches within the modeled landscape. This allowed me to observe theoretical changes in population size due to resource confinement and also to determine the ideal cell within the landscape for supporting colonies under different theoretical mowing regimes.

I found that overall environments that were completely unmowed were able to support more colonies of *B. impatiens* than any other model. Environments where roadsides were mowed

were able to support colonies of *B. impatiens* at 96.95% of the average density found in unmowed environments. Environments where meadows were mowed supported 87.92% of the average density of unmowed environments. Environments where both roadsides and meadows were mowed supported 77.09% of the average density of unmowed environments.

I found that environments in unmowed conditions (Table 2) support populations of *B. impatiens* at an average of 17.64 across the entire landscape. This variation of the model showed that LC 14 most frequently had the highest density of colonies at a rate of three out of five. The other iterations of the model showed that LC 7 and LC 12 had the highest average density of colonies for one iteration each.

I found that environments where roadsides were mowed (Table 3) supported populations of *B. impatiens* at an average of 17.10 colonies across the entire landscape. Landscape cell (LC) 13 most frequently had the highest average colony density for this model variation at a rate of three out of five iterations. The other two iterations of this model showed LC 15 and LC 16 having the highest colony density for one iteration each.

I found that environments where roadsides were left unmowed and meadows were mowed (Table 4) supported populations of *B. impatiens* at an average of 15.51 colonies across the entire landscape. This variation of the model showed that LC 2, LC 3, LC 6, LC 13, and LC 14 each had the highest density of colonies for one iteration.

I found that environments where roadsides and meadows were mowed (Table 5) supported populations of *B. impatiens* at an average of 13.60 colonies across the entire landscape. This variation of the model showed that LC 2, LC 6, LC 9, LC 10, and LC 14 each had one iteration where they supported the highest density of colonies.

The second output of this model that I tracked for analysis was the overall resources produced under different mowing regimes. I tracked the resources produced for the duration of the season as maximum grams of nectar on a peak flowering day across the entire landscape as well as in individual cells. My model predicted that on a peak day in unmowed environments that an average of 25.90 grams of sugar were produced across the landscape by my focal species. On a peak day in environments where only roadsides were mowed my model predicted that an average of 12.92 grams of sugar can be produced across the landscape by my focal species. This is 49.90% as much sugar as was produced by the unmowed model. On a peak day in a landscape where only meadows were mowed my model predicted that an average of 2.16 grams of sugar could be produced by my focal species across the landscape. This is 8.36% as much sugar as was produced in the unmowed model. On a peak day in a landscape where both roadsides and meadows were mowed my model predicted that my target species would produce an average of 0.15 grams of sugar across the landscape. This is 0.57% as much sugar as was produced in the unmowed model.

When comparing the production of peak resources in the model to total colonies found within the landscape I found that they could be displayed as an exponential relationship with the following equation:

$$y = 1.56 \cdot 10^{-8} \cdot e^{1.2x}$$

(Fig. 2; R^2=0.999)

where nectar resources needed to support colonies grows exponentially as colony numbers increase.

The unmowed models (Table 2) showed that resources produced by my focal species during the first portion of the flowering season (RP1) was highest on average in LC 14. This cell also most frequently showed the highest resources produced during the flowering period at a rate of four out of five iterations. LC 13 also showed one iteration where RP1 was highest in that cell. For the resources produced in the second portion of the season by my focal species (RP2) the model showed that LC 14 produced the most resources on average and showed the highest RP2 value in three out of five iterations. The other two iterations showed that LC 13 produced the highest RP2 value. The unmowed model showed that colonies in LC 14 produced the most workers on average (W) and the most workers in three out of five iterations in the model. The other two iterations that produced the highest W value were one each from LC 6 and LC 15. The number of colonies found in a cell (C) was highest on average in LC 10. LC 14 showed the highest C value in three out of five iterations. The other two iterations of the model showed that LC 6 and LC 12 had the highest C value for one iteration each.

The roadside mowed models (Table 3) showed that resources produced by my focal species during the first portion of the flowering season (RP1) was highest on average in LC 14. The cells that showed the highest resources produced during the flowering period were LC 14 at a rate of four out of five iterations and LC 13 at one iteration. For the resources produced in the second portion of the season by my focal species (RP2) the model showed that LC 14 produced the most resources on average. The cells that had the highest RP2 value were LC 14 at four out of five iterations and one iteration showed that LC 13 produced the highest RP2 value. The model showed that colonies in LC 11 produced the most workers on average (W). The iterations that produced the highest W value were from LC 13 at three out of five iterations, LC 15 at one

iteration, and LC 16 at one iteration. The number of colonies found in a cell (C) was highest on average in LC 11. The cells that produced the highest C value were LC 13 at five out of five iterations, LC 15 at one iteration, and LC 16 at one iteration.

The meadow mowed models (Table 4) showed that resources produced by my focal species during the first portion of the flowering season (RP1) was highest on average in LC 14. The cell that showed the highest resources produced during the flowering period was LC 14 at a rate of five out of five iterations. For the resources produced in the second portion of the season by my focal species (RP2) the model showed that LC 14 produced the most resources on average. The cells that had the highest RP2 value were LC 14 at four out of five iterations and one iteration showed that LC 9 produced the highest RP2 value. The model showed that colonies in LC 13 produced the most workers on average (W). The iterations that produced the highest W value were from LC 2 at 1 iteration, LC 6 at one iteration, LC 13 at one iteration, and LC 14 at two iterations. The number of colonies found in a cell (C) was highest on average in LC 13. The cells that produced the highest C value were LC 2, LC 3, LC 6, LC 13, and LC 14 at one iteration each.

The roadside and meadow mowed models (Table 5) showed that resources produced by my focal species during the first portion of the flowering season (RP1) was highest on average in LC 14. The cell that showed the highest resources produced during the flowering period was LC 14 at a rate of five out of five iterations. For the resources produced in the second portion of the season by my focal species (RP2) the model showed that LC 14 produced the most resources on average. The cell that had the highest RP2 values was LC 14 at five out of five iterations. The model showed that colonies in LC 14 produced the most workers on average (W). The iterations

that produced the highest W value were from LC 2, LC 6, LC 9, LC 10, and LC 14 at one iteration each. The number of colonies found in a cell (C) was highest on average in LC 14. The cells that produced the highest C value were LC 2, LC 6, LC 9, LC 10, and LC 14 at one iteration each.

DISCUSSION

The results of this model predict that different mowing practices will yield different outcomes for populations of *B. impatiens*. The decline in colony density seen when mowing is implemented was universal across all model iterations. There was never an instance when mowing enhanced pollinator populations or allowed populations to persist at a level that was consistent with a landscape that left unmowed. This is unsurprising since values for resource production were derived from peak abundance data that consistently showed a detriment to flower abundance due to mowing and the equations used to project bee abundance included a sensitivity to resource term. This result is consistent with multiple bumble bee abundance models that incorporate resource intake which show a general reduction of queens produced by a colony when flower resources are sparse (Crone & Williams 2016, Haussler et al. 2017, Becher et al. 2018). This suggests that mowing relatively large areas of land has the potential to reduce floral resources to the point that individual colony fecundity is influenced. Empirical studies involving live colonies are required to appropriately assess the impacts of mowing on bumble bee abundance dynamics.

The model variations showed different gradients of decline based on which mowing strategy was projected. This is partially supported by a previous empirical study conducted in

suburban lawns that found that different mowing frequencies allowed pollinators different access to flower resources. The study found that flower abundance declined along a gradient with mowing frequency, but that pollinator abundance was highest with a moderate mowing frequency. The proposed mechanism for this being that infrequent mowing allowed pollinators to more easily locate and manipulate the flowers by clearing extraneous foliage (Lerman, Contosta, Milam & Bang 2018).

Declines in bumble bee abundance due to mowing only roadside areas were considerably less than the declines when mowing was projected on only meadow areas. This is partially due to the flower density difference between the habitat types incorporated into the model, and partially from the difference in cover area between the habitat types within the modelled landscape. This suggests that given the choice to mow one or the other of these habitat types that supporting pollinators is better accommodated by mowing roadsides. This is consistent with findings from empirical studies which have shown that the proportion of managed and unmanaged area within a landscape influences the abundance of pollinators (Carvell et al. 2011, Winfree, Aguilar, Vazques, LeBuhn & Aizen 2009, Holzschuh et al. 2016, Smith et al. 2016). The difference between implementing mowing on roadsides and meadows is likely due to a combination of factors.

I found that there was no single cell within the landscape that constantly supported the highest density of colonies, but there were trends that differed among the model variations. The frequency at which particular cells supported the highest density was dependent on which mowing strategy was implemented. This is consistent with other bumble bee abundance models that consider spacial influences and resource factors in that as resource distribution changes, so

does the local abundance of bees (Becher et al. 2018). This suggests that changes in mowing practices could influence the distribution of bumble bee colonies within the landscape through eliminating large resource patches. This effect would be more pronounced through implementing mowing across meadows within the landscape. This is consistent with other empirical studies that have shown that the abundance of pollinators within a landscape is greater in areas near flower resource patches (Kallioniemi et al. 2017).

This model, and others like it, have the ability to provide valuable predictions for creating strategies that support populations of bumble bees on a variety of spatial scales. This model in particular shows that *Bombus impatiens* is best supported through implementing a no-mow strategy throughout the flowering season. There is evidence from the literature that suggests that flower abundance throughout the lifecycle of bee colonies contributes to the ability of these pollinators to persist (Timberlake et al. 2019). As such, mowing during the flowering season could cause resource gaps. Leaving the areas completely unmanaged may not be the best option either. Studies have shown that when managing grassy roadside areas that mowing the foliage twice during each flowering season and clearing the dried plant matter from the areas produced greater pollinator abundance than did unmanaged grassy areas or mowing a single time during each flowering period (Noordijk, Delille, Schaffer & Sykora 2009). This is counter to the outcome produced by my model, but was conducted in a different area and with different mowing frequencies. This suggests that further research is needed to determine what is the most ideal mowing policy for supporting pollinators in general and bumble bees specifically. Such an experiment would require an expansive area and a small fleet of mowing equipment coupled with pollinator abundance observations.

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TABLES

Parameter	Description	Unit	Value
n_{max}	Number of nests in a cell of maximum quality	nests/ha	19.6
β	Mean dispersal distance of foraging	m	530
β_d	Mean dispersal distance to nesting habitat	m	1000
a_w	Mean growth rate for workers	-	100 (a)
b_w	Sensitivity of worker production to resource chance	-	50 (a)
a_q	Mean growth rate for queens	-	100 (a)
b_q	Sensitivity of queen production to resource change	-	50 (a)
w_{max}	Maximum number of workers from single colony	-	600
q_{max}	Maximum number of queens from single colony	-	160
ρ_F	Survival rate per distance foraging	-	0.8 (a)
P_N	Survival rate per distance dispersing for nesting	-	0.85 (a)

Table 1: Model parameter descriptions and values. Arbitrarily estimated values marked as (a).

RP1: 0.083 RP2: 0.636 RT: 0.719 W: 12.785 C: 3.506	RP1: 0.080 RP2: 0.610 RT: 0.690 W: 12.228 C: 3.356	RP1: 0.077 RP2: 0.747 RT: 0.824 W: 12.077 C: 3.349	RP1: 0.071 RP2: 0.978 RT: 1.049 W: 12.145 C: 3.425
RP1: 0.107 RP2: 1.121 RT: 1.228 W: 11.855 C: 3.295	RP1: 0.085 RP2: 0.928 RT: 1.013 W: 12.830* C: 3.576 *	RP1: 0.083 RP2: 1.071 RT: 1.154 W: 12.554 C: 3.529	RP1: 0.096 RP2: 1.519 RT: 1.615 W: 12.644 C: 3.588
RP1: 0.180	RP1: 0.128	RP1: 0.118	RP1: 0.123

RP2: 1.992 RT: 2.172 W: 12.843 C: 3.587	RP2: 1.515 RT: 1.644 W: 13.364 C: 3.736	RP2: 1.619 RT: 1.737 W: 12.577 C: 3.547	RP2: 1.973 RT: 2.095 W: 12.752 C: 3.623 *
RP1: 0.208 * RP2: 2.620 ** RT: 2.828 ** W: 12.535 C: 3.521	RP1: 0.271 **** RP2: 2.822 *** RT: 3.093 *** W: 13.218 *** C: 3.684 ***	RP1: 0.152 RP2: 1.897 RT: 2.049 W: 13.140 * C: 3.697	RP1: 0.120 RP2: 1.869 RT: 1.989 W: 12.046 C: 3.417

Table 2: Unmowed model output visualization for comparing average values: 1) nectar resources produced during the first period of the season (RP1), 2) nectar resources produced during the second period of the season (RP2), 3) total resources produced (RT), 4) workers produced (W), and 5) colonies successfully established (C). Highest values frequencies for iterations are marked by asterisks.

RP1: 0.031 RP2: 0.275 RT: 0.306 W: 11.396 C: 3.161	RP1: 0.031 RP2: 0.282 RT: 0.313 W: 12.182 C: 3.379	RP1: 0.040 RP2: 0.376 RT: 0.416 W: 11.131 C: 3.090	RP1: 0.056 RP2: 0.533 RT: 0.589 W: 12.017 C: 3.338
RP1: 0.051 RP2: 0.493 RT: 0.545 W: 12.618 C: 3.503	RP1: 0.048 RP2: 0.436 RT: 0.484 W: 11.884 C: 3.300	RP1: 0.055 RP2: 0.535 RT: 0.591 W: 11.319 C: 3.144	RP1: 0.080 RP2: 0.788 RT: 0.867 W: 12.211 C: 3.392
RP1: 0.094 RP2: 0.905 RT: 0.998 W: 12.760 C: 3.541	RP1: 0.075 RP2: 0.698 RT: 0.773 W: 12.173 C: 3.380	RP1: 0.085 RP2: 0.815 RT: 0.900 W: 13.480 C: 3.744	RP1: 0.106 RP2: 1.027 RT: 1.133 W: 12.936 C: 3.592
RP1: 0.127 * RP2: 1.249 * RT: 1.375 * W: 13.175 *** C: 3.658 ***	RP1: 0.142 **** RP2: 1.363 **** RT: 1.505 **** W: 12.535 C: 3.479	RP1: 0.101 RP2: 0.958 RT: 1.060 W: 13.180 * C: 3.660 *	RP1: 0.096 RP2: 0.973 RT: 1.069 W: 12.072 * C: 3.352 *

Table 3: Roadside mowed model output visualization for comparing average values: 1) nectar resources produced during the first period of the season (RP1), 2) nectar resources produced during the second period of the season (RP2), 3) total resources produced (RT), 4) workers

produced (W), and 5) colonies successfully established (C). Highest values frequencies for iterations are marked by asterisks.

RP1: 0.048 RP2: 0.109 RT: 0.157 W: 11.824 C: 3.050	RP1: 0.046 RP2: 0.107 RT: 0.154 W: 12.208 * C: 3.149 *	RP1: 0.030 RP2: 0.070 RT: 0.100 W: 12.506 C: 3.227 *	RP1: 0.019 RP2: 0.042 RT: 0.061 W: 11.796 C: 3.043
RP1: 0.046 RP2: 0.103 RT: 0.149 W: 12.469 C: 3.218	RP1: 0.034 RP2: 0.078 RT: 0.112 W: 12.539 * C: 3.236 *	RP1: 0.022 RP2: 0.051 RT: 0.073 W: 12.170 C: 3.141	RP1: 0.016 RP2: 0.037 RT: 0.053 W: 11.342 C: 2.926
RP1: 0.078 RP2: 0.179 * RT: 0.257 W: 11.401 C: 2.942	RP1: 0.050 RP2: 0.115 RT: 0.165 W: 11.441 C: 2.952	RP1: 0.030 RP2: 0.065 RT: 0.095 W: 12.069 C: 3.113	RP1: 0.017 RP2: 0.039 RT: 0.057 W: 11.883 C: 3.065
RP1: 0.063 RP2: 0.140 RT: 0.203 W: 12.652 * C: 3.265 *	RP1: 0.101 ***** RP2: 0.228 **** RT: 0.329 ***** W: 12.241 ** C: 3.161 *	RP1: 0.040 RP2: 0.092 RT: 0.132 W: 12.400 C: 3.199	RP1: 0.020 RP2: 0.047 RT: 0.067 W: 11.353 C: 2.929

Table 4: Meadow mowed model output visualization for comparing average values: 1) nectar resources produced during the first period of the season (RP1), 2) nectar resources produced during the second period of the season (RP2), 3) total resources produced (RT), 4) workers produced (W), and 5) colonies successfully established (C). Highest values frequencies for iterations are marked by asterisks

RP1: 0.002 RP2: 0.009 RT: 0.011 W: 10.057 C: 2.675	RP1: 0.002 RP2: 0.008 RT: 0.010 W: 10.143 * C: 2.698 *	RP1: 0.002 RP2: 0.007 RT: 0.008 W: 9.355 C: 2.490	RP1: 0.001 RP2: 0.003 RT: 0.004 W: 10.027 C: 2.668

RP1: 0.002 RP2: 0.008 RT: 0.010 W: 10.144 C: 2.699	RP1: 0.002 RP2: 0.006 RT: 0.008 W: 10.106 * C: 2.690 *	RP1: 0.001 RP2: 0.004 RT: 0.005 W: 10.486 C: 2.790	RP1: 0.001 RP2: 0.003 RT: 0.004 W: 10.394 C: 2.766
RP1: 0.003 RP2: 0.012 RT: 0.014 W: 10.432 * C: 2.776 *	RP1: 0.002 RP2: 0.009 RT: 0.011 W: 10.392 * C: 2.764 *	RP1: 0.001 RP2: 0.005 RT: 0.011 W: 10.696 C: 2.846	RP1: 0.001 RP2: 0.003 RT: 0.004 W: 9.893 C: 2.633
RP1: 0.003 RP2: 0.011 RT: 0.014 W: 10.632 C: 2.831	RP1: 0.005 ***** RP2: 0.019 ***** RT: 0.023 ***** W: 10.773 * C: 2.868 *	RP1: 0.002 RP2: 0.007 RT: 0.009 W: 10.211 C: 2.717	RP1: 0.001 RP2: 0.004 RT: 0.005 W: 9.767 C: 2.600

Table 5: Meadow and roadside mowed model output visualization for comparing average values: 1) nectar resources produced during the first period of the season (RP1), 2) nectar resources produced during the second period of the season (RP2), 3) total resources produced (RT), 4) workers produced (W), and 5) colonies successfully established (C). Highest values frequencies for iterations are marked by an asterisk.

FIGURES

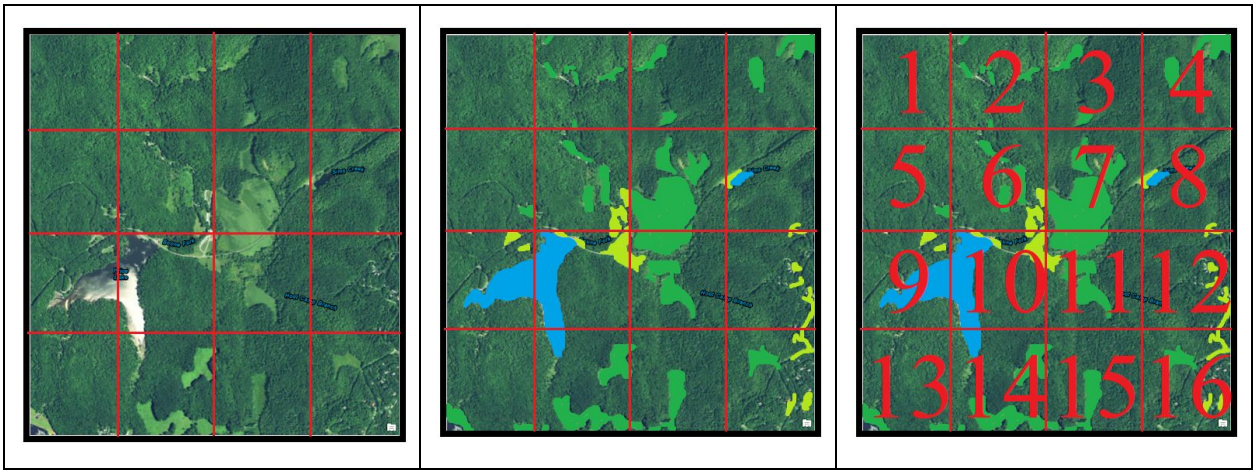

Figure 1: The figures show a visualization of defining cover type of the areas (green:meadow, yellow:roadside, blue:water, uncolored:wooded). It also shows the naming scheme for landscape cells (LC).

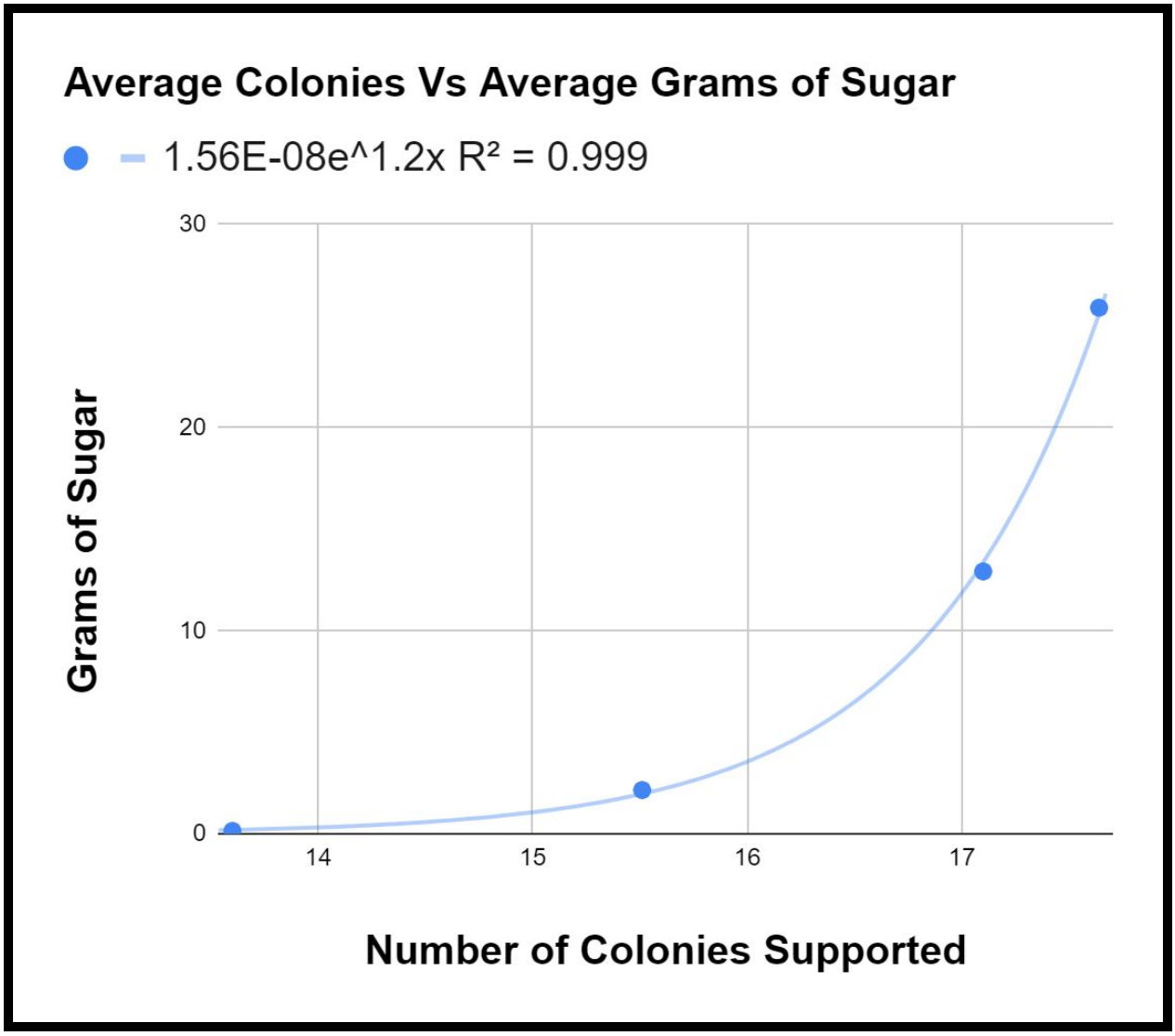

Figure 2: A graphic of the exponential equation used to represent the relationship between grams of sugar produced by focal species and number of colonies found within the projected landscape. Relationship presented between average values across all mowing treatment models.

APPENDIX 1: NECTAR ANALYSIS SUPPLEMENTARY DATA

I conducted a collaborative laboratory experiment with an undergraduate student where samples of my target flowers (with the exception of *M. clinopodia* due to sampling restrictions) were placed in pollinator excluding bags for twenty-four hours. The white clover *Trifolium repens* was also analyzed. These flowers then had nectar analysis performed on them using a wash method to determine the average sugar content produced by a single inflorescence in a period of twenty-four hours. The evidence provided by this experiment show that my target plant species are variable in their single inflorescence nectar production rates. This variation in nectar production among target flower species becomes even more drastic when considered on the landscape level due to the additional factor provided by the differences among species for number of flowers per inflorescence and number of inflorescences per square meter.

Quantifying Nectar Resources

Individual inflorescences were placed in pollinator excluding mesh for a period of twenty four hours. After the exclusionary period the inflorescences were cut and taken immediately for nectar collection. The nectar was analyzed using methods from (McKenna and Thomson 1988) to give relative nectar production rates from my target plant species for use in my ecological model.

Nectar Production Rates

Asclepias syriaca	*Trifolium pratense*	*Trifolium repens*	*Solidago rugosa*	*Prunella vulgaris*
0.510	0.0262	0.0452	0.106	0.189

Table 11: Average twenty-four hour nectar production rate for a single inflorescence of five flower species in grams of sugar.

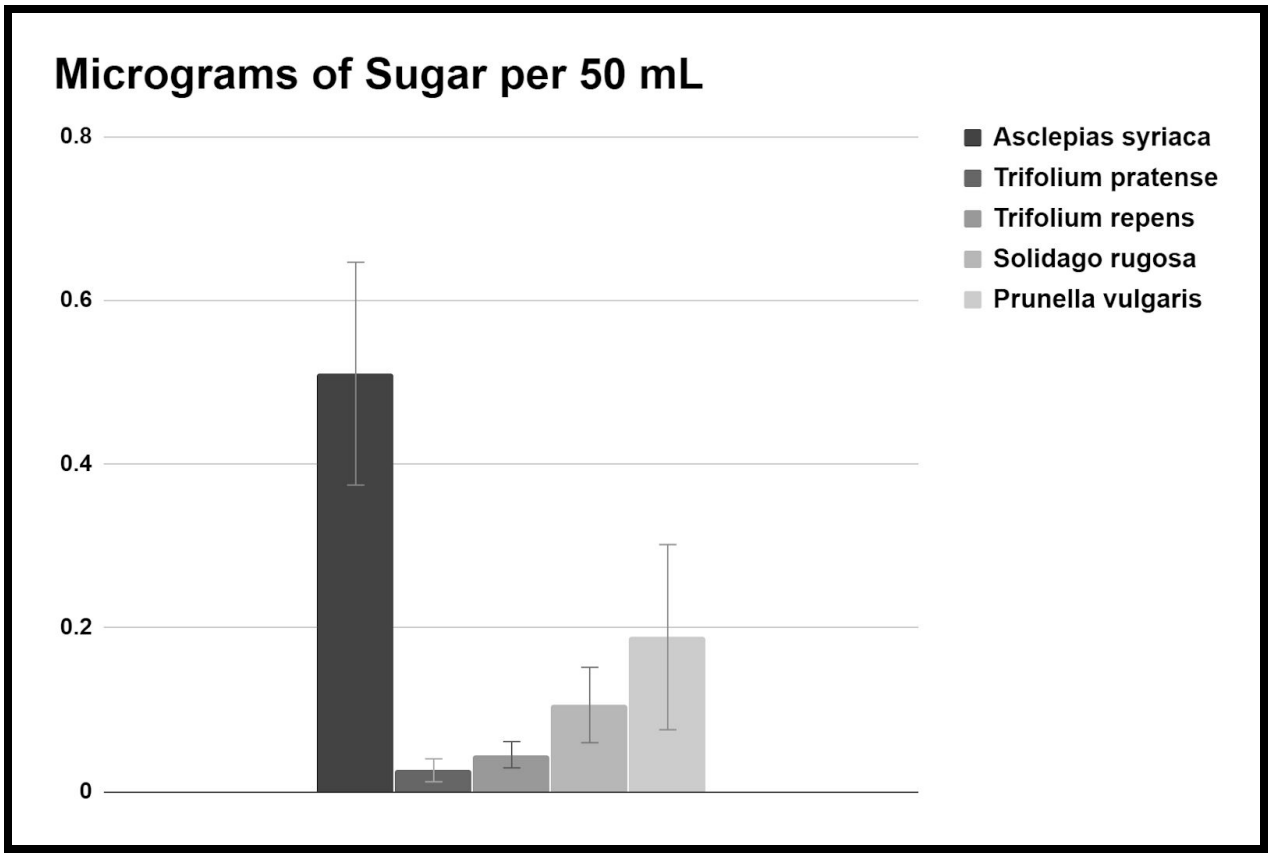

Figure 7: Average twenty-four hour nectar production rate for a single inflorescence of five flower species.

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VITA

William Vannoy was born and reared in Taylorsville, North Carolina. He graduated from Alexander Central High School in May, 2012. In August of that year he enrolled at Appalachian State University where he studied Secondary Science Education. In May of 2016 Mr. Vannoy graduated from Appalachian State with a Bachelor of Science degree. In September of 2016 he once again enrolled at Appalachian State University to pursue a Master of Science in Ecology and Evolution. In December of 2019 the M.S was awarded.

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